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THE MECHANISM OF CROSSING-OVER

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IT is the object of this paper to give an account of the most important evidence thus far gained in regard to the manner in which separation of linked factors—often interpreted as "crossing-over"—takes place, and to describe an experiment in which a new method for studying the occurrence of such separation is employed. This experiment is still under way, but as it may be a considerable time before the results are obtained in full, it would not be advisable to withhold longer an account of this work and of other work that bears on the nature of the "crossing-over."

I. THE DISCOVERY OF INTERCHANGE BETWEEN HOMOLOGOUS CHROMOSOMES

The question as to whether separation of linked factors is due to pieces of homologous chromosomes changing places with each other, carries us back to the question whether the factors lie in the chromosomes at all. As is well known, there is a large body of evidence from cytology and from experimental embryology, showing that the chomosomes are persistent, self-perpetuating structures which have a profound influence upon development. But the first definite evidence that the Mendelian factors are contained in the chromosomes lay in the striking correspondence which was found between their respective

methods of distribution—the segregation of Mendelian allelomorphs exactly paralleling the pairing and separation of homologous chromosomes during the maturation of the germ cells, and the random assortment of Mendelian factors belonging to different, independently segregating pairs, paralleling the random assortment of chromosomes belonging to different pairs (Sutton). Still, there was no indication of a connection between any particular chromosome and a particular character until the work of McClung, Stevens and Wilson and others proved that in many animals the "X-chromosome" contains, or at least invariably accompanies, a factor for sex, inasmuch as all fertilized eggs which receive two X-chromosomes develop into females, while those with one X become males.

The next time that particular factors and chromosomes were found to be correlated was in 1910, when Morgan pointed out that the factor in *Drosophila* determining whether an individual shall have red or white eyes, as well as several other factors, must also be located in the X-chromosome (or at least must *accompany* it in its segregation). For, to put the whole argument briefly, the fact that a red-eyed male bred to a white-eyed female produces red-eyed daughters and white-eyed sons shows that the female-producing spermatozoa—those that receive the X-chromosome—also receive the factor for red, but the male-producing sperm—which do not receive the X— also fail to receive red. In other words, the factor for red was judged to be in the X-chromosome, because in the male it is always distributed to precisely the same spermatozoa as those to which the X's happen to be distributed. Bridges has recently obtained evidence that in the female, too, such "sex-linked" factors accompany the X-chromosome in segregation. Ordinarily there is no opportunity for attacking this question in the female, since the female contains two X's, which are of course indistinguishable to the eye, so that it would be impossible to tell whether or not a particular one of the X's was always distributed to the

same eggs as a particular sex-linked factor. But in Bridges's cases of non-disjunction, the maturation divisions are often abnormal, so that some eggs are found to have retained both X's; and in accordance with this it is found that some of the offspring of such females have likewise received two sets of maternal sex-linked factors. These cases, therefore, show that in the female also the sex-linked factors "follow" the X-chromosome (1, 2).

Morgan next studied the relation of different sex-linked factors to each other in inheritance, and then another remarkable fact came to light. Theoretically, the dihybrid females resulting from a cross of a red-eyed fly having rudimentary wings by a white-eyed fly having long wings (both of these pairs of characters are sex-linked) should have contained in one of their two X-chromosomes the factors "red" and "rudimentary," and in the homologous X-chromosome the factors "white" and "long"; the mature eggs should retain either one X or the other and should therefore have contained either red and rudimentary or white and long. In other words, red and rudimentary should be *completely linked* in their inheritance, and similarly white and long. But the results showed that these factors sometimes separate in heredity, for not only the above types of offspring are produced, but also some red longs and white rudimentaries (7); in fact, about 42 per cent. of the offspring belong to one or the other of the two latter classes. If we admit that white and long were originally present in the same chromosome, the *only* way to account for this separation of the factors is to suppose that in some of the cells of the hybrid female the X-chromosomes interchanged parts before being distributed to the eggs. For if the factor for "long" of the chromosome containing "white" and "long" should somehow change places with the "rudimentary" of the homologous chromosome, then when homologous chromosomes are separated at the maturation division, the egg may come to contain either an X-chromosome with white and rudimentary or an X with red and long.

Recent work on *Drosophila* has borne out in a striking way the conclusion that the separation of factors just discussed is due to chromosomal interchange. It will be remembered that the pairs of factors in the example underwent recombination in only about 42 per cent. of the eggs, *i. e.,* they held together more often than they separated, and so might be said to be *partially linked.* Their mode of inheritance therefore forms a contrast not only to complete linkage, but also to the familiar cases of random assortment, where two pairs of factors are found recombined in about 50 per cent. of the offspring, and thus show no linkage at all, presumably because they lie in different pairs of chromosomes which segregate independently. Further investigation showed that not only "white" and "rudimentary," but all the known sex-linked factors, instead of segregating independently, are "partially linked" to one another in greater or less degree. This then was additional evidence that these factors did not lie in different pairs of chromosomes, as in familiar cases, but in the same pair of chromosomes, and that their separation or recombination was therefore dependent upon chromosomal interchange. But furthermore, if these linked factors all lie in the X-chromosome (being sex-linked), then it might be expected that other groups of interlinked factors also would be found, that lie in other chromosomes. A factor in any one of these other groups would not be sex-linked, but would be linked in greater or less degree to every other factor of the same group, since it lay in the same chromosome with it, but it would undergo 50 per cent. of recombination with factors in other groups. This expectation has been fulfilled. In 1911 Morgan and Lynch found two pairs of factors in *Drosophila* (black versus gray body color; vestigial *vs.* long wings) that were linked to each other, but that were not sex-linked (10). These were designated as lying in group II or Chromosome II. Later, Sturtevant found that two other pairs of factors (pink *vs.* red eyes and ebony *vs.* gray body color) were also linked to each other, but were neither sex-linked nor linked to the

other non-sex-linked group; these were assigned to Group III or Chromosome III (15). Incidentally, it was evident that these cases are of exactly the same nature as those previously discovered by Bateson and Punnett in the sweet pea, and termed by them "coupling" or "repulsion." Moreover, the chromosome interpretation made it clear why the factors should be "coupled" or "repelled" according to whether the hybrid received them from the same or from opposite parents. There was only one difference in detail between the facts in the two species: it was discovered by Morgan that in *Drosophila* the linkage is always complete in the male, the separation of factors that are linked to each other occurring only in the female (9); in the plants, on the other hand, recombination occurs in the genesis both of eggs and of sperm.

Since that time the inheritance of over one hundred pairs of factors of *Drosophila* has been studied. This investigation should give an extensive experimental test of the theory of chromosomal interchange, for if linked factors are those carried by the same chromosome, there should be the same number of groups of interlinked factors as there are pairs of chromosomes. There are *four* pairs of chromosomes in *Drosophila*—two pairs of long ones, the pair of moderately long sex-chromosomes, and a pair of very small chromosomes. By 1913, work had been done upon a large number of factors, and the results showed *that all these factors were linked in one of the three groups already discovered.* But in 1914 the author found a pair of factors independent of these (bent *vs.* straight wing), *i. e.,* constituting Group IV (12), and not long afterwards Miss Hoge found another pair of factors in this fourth group (eyeless *vs.* normal eye), (3). Accordingly, the number of groups and of chromosomes now correspond, and not only that, but the relative sizes of the groups correspond in a general way with the relative lengths of the chromosomes. Can it be mere chance that one hundred factors fall into this particular grouping? But if it is admitted that these groups are carried in the

chromosomes, then, as above pointed out, the separation of factors in a group means chromosomal interchange.

II. A Mechanism of Interchange already provided by the Theory of Crossing-Over (Chiasmatype)

Janssen's "chiasmatype theory," based on cytological observations of spermatogenesis in *Batracoseps*, described just such a process of interchange between the homologous chromosomes as Morgan's evidence from genetics required (4). A great bulk of evidence has accumulated to show that during the period of synapsis, homologous chromosomes come into contact, and in many cases chromosomes can be seen to be twisted around each other during one stage or another of synapsis. The essential point postulated by the chiasmatype theory is that, as the paired chromosomes draw apart again, they do not always untwist completely, but may break at some points where they are crossed—thus, in Fig. 1, the upper piece of the light-colored chro-

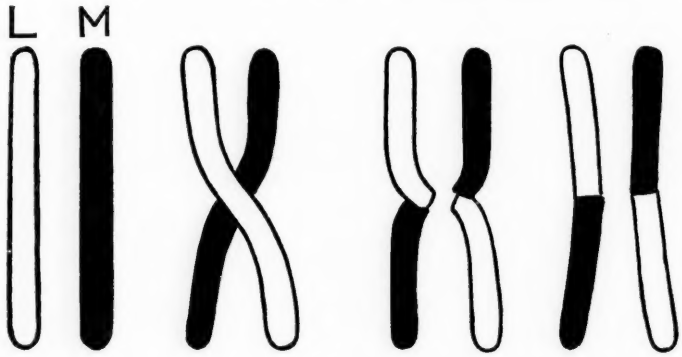

FIG. 1.

mosome (L), which was on one side, loses its connection with the lower part of L, that has crossed to the other side, but becomes united instead with the lower piece of the dark chromosome (M) which, on account of the crossing of the strands, now follows it on the same side; similarly, of course, the upper part of M becomes united with the

lower part of L; in this way a recombination of parts is accomplished. Morgan and other workers on *Drosophila* base their acceptance of this essential point in Janssens's chiasmatype theory upon the evidence (from cytology) that homologous chromosomes do twist about each other during synapsis, taken together with the evidence (from genetics) that these chromosomes emerge as new combinations. Janssens, on the other hand, maintains that certain details in the appearance of the chromosomes during that stage in synapsis called "strepsinema" give ocular evidence that crossing-over occurs at this particular period and in a particular manner. As it would seem possible, however, to put another interpretation upon his figures, this question may be deferred until later.

Janssens had intended the chiasmatype theory to explain the supposed fact that there might be more pairs of factors

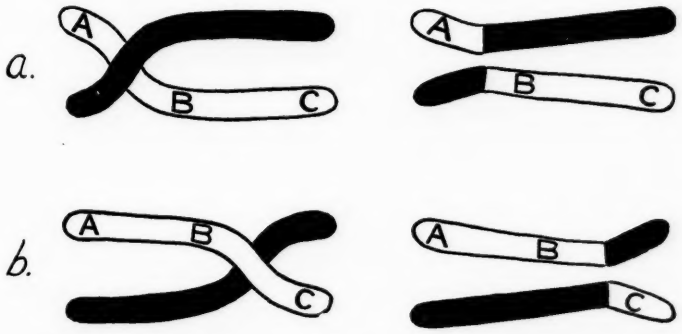

FIG. 2.

capable of recombination than there were pairs of chromosomes. (It might be mentioned in passing, however, that at that time this fact had not yet been demonstrated; there are even now probably no published facts except those recently discovered in *Drosophila* which prove this point). As shown above, Morgan went further than this with the chiasmatype theory by applying it to explain, specifically, the recombination of *linked* factors (8). Moreover, he pointed out at the same time an important corol-

lary to this theory. It has already been stated that he had found different degrees of linkage to exist between the various factors of a group: for example, the proportion of cases in which separation occurs between white and rudimentary was said to be 42 per cent., whereas the frequency of separation between white (eye color) and the factor for yellow body color is only about 1 per cent. In explanation of these different degrees of linkage, Morgan pointed out that, on the chiasmatype theory, the closer the proximity of two factors to each other in the chromosome, the smaller would be their frequency of separation, for the less would be the chance for a crossing-over of the chromosomes to occur *between* them. Thus, in Fig. 2, the factors A and C become separated both in case (*a*) and in case (*b*), because A and C lie so far apart that in both cases the point of crossing-over falls between them, but in only one of the cases do A and B separate, and in one case B and C, since these are so near together that the point of crossing-over may often be beyond instead of between them. In other words, on the chiasmatype theory, frequency of recombination must be, to a certain extent at least, an index of the distance apart of factors along the chromosome. Since the time when these ideas were proposed (1911), two important series of facts have come to light in the studies on *Drosophila,* in support of the chiasmatype theory of interchange and of these extensions of it.

III. A Verification of the Theory of Crossing-Over. The Law of Linear Linkage

It occurred to Sturtevant in 1911 that, if the factors are carried in the chromosomes, then, *owing to their linear arrangement,* the distance along the chromosome between any two factors (A and C) must be either the sum or the

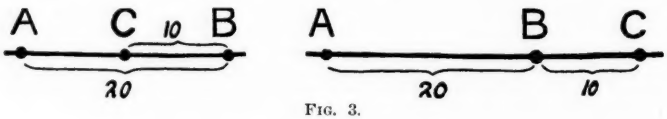

FIG. 3.

difference of their distances from any third factor (B) of the same group, *i. e.*, length AC = length AB ± length BC, the + or − depending on whether the third factor is between or beyond the other two (see Fig. 3). Accordingly, if, as Morgan suggested, the frequencies of separation (linkage values) between factors depend on their distances apart, then the frequency of separation (degree of linkage) between the two factors, A and C, should be predictable, given the frequency of separation of each from the third factor, B. To put the matter diagrammatically, A, B and C have been represented in figure 3 as points along a line; A and B, we will suppose, separate from each other in heredity in 20 per cent. of cases, to correspond with which they have been placed the same number of units (20) apart in the diagram; similarly, B and C, which we will suppose to separate 10 per cent. of the time, have been placed 10 units apart. (As above pointed out, there are obviously two possible diagrams to choose between, depending on whether C is beyond A and B or between them.) Then, if it be true that the frequency of separation between any factors is always precisely proportional to their distance apart, it will follow that the per cent. of separations between A and C will be equal to the number of units of distance on our diagrammatic chromosome between A and C; this in turn equals AB ± BC = 30 or 10. If separation frequency bears a less simple relation to distance, but is nevertheless determined by it (see below), frequency AC will not *equal* distance AC (*i. e.*, AB ± BC) but can be *calculated* from the latter. On the other hand, if our premises are false, and there is no linear relation at all between the factors that determine their frequency of separation, then frequency AC will not be equal to diagram distance AC (*i. e.*, to AB ± BC), nor even, in the case of different sets of factors, will it bear any constant relation to diagram distance AC; that is, it would not be possible to discover any constant rules for calculating the third frequency from the two others which will hold, even approximately, for various sets of factors (BCD, LMN, etc.).

Sturtevant found that there is indeed a linear relation in the frequencies of separation (14, 16). In the case of smaller per cents. of separation, per cent. AC always is precisely equal to the sum or difference of per cents. AB and BC (within the limits of probable error), so that the per cents. of separation for all combinations of these factors is accurately represented by a linear diagram. In the case of higher per cents. of separation (long distances), the highest of the three frequencies (let us call it AC) falls short of the sum of the other two (AB + BC), and so it is a smaller number than the distance representing it on the diagram, but it nevertheless (within the normal limits of error) can be calculated from this diagram distance AC, for a constant relation was discoverable between this hypothetical distance and the actual frequency. Thus the different frequencies do not bear any random relation to each other that is mathematically possible, but bear relations that disclose a linear connection between the factors.

It remains to consider the meaning of the fact that in cases where there is a high per cent. of separations, the highest per cent.—that between A and C, let us say—is not as great as the value of the distance AC representing it on the diagram, *i. e.*, it is less than the sum of the per

FIG. 4.

cents shown between A and B, and B and C, respectively. If, whenever A and B or B and C separate, A and C separate also, as shown in Fig. 2, (*a*) and (*b*), then per cent. AC would be equal to per cent. AB plus per cent. BC, but since per cent. AC is lower than this, there must be cases in which, although A and B or B and C separate, A and C fail to separate. It is obvious that in these cases, where B separates from A but A does not separate from C, that B

must have separated from C also, *i. e.*, a separation has occurred between A and B, and between B and C, coincidentally. On the view above presented, a separation means a crossing-over of chromosomes, and so in these cases the chromosomes must be thought of as crossing-over at two points coincidentally, as shown in Fig. 4. This process has been named by Sturtevant "double crossing-over." As shown in the figure, where crossing-over occurs coincidentally, both in AB and in BC, the chromosome crosses and crosses back again between A and C, hence the latter factors do not become separated.

When the frequencies of separation (diagram distances) between A and B, and between B and C are both small, it is to be expected as a matter of pure chance, if the factors are joined in line in the manner described, that such coincidences will occur very rarely, even in proportion to the small frequencies involved, and so the per cent. of separations between A and C will be practically as great as that between A and B plus that between B and C. Hence per cent. AC will be accurately represented by diagram distance AC. On the other hand, if separation is frequent between A and B or between B and C, there should be more chance of coincidence of these separations, and the number of separations between A and C will fall correspondingly short of AB + BC, which is the value of AC shown on the diagram. Consequently, in predicting frequency AC on the basis of AB and BC, allowance must be made for these coincidences. But the author ventures to point out that, as the number of these coincident separations is found to be largely determined by the frequency of separation, greater frequencies being accompanied by a larger proportion of coincidences, as has been shown, then the amount of allowance to be made can be approximately calculated for any given distance on the diagram; accordingly, the frequency of separation between A and C can be calculated from AB + BC, *i. e.*, from the distance AC on the diagram. The precise manner in which coincidence of separations increases with their frequency is a

question which will be reserved until later. But it is clear that, since coincidence does not vary independently of "distance," a linear relation holds between the linkage values, in that these values can be calculated from a linear diagram much more exactly than would be expected on chance relationships; in mathematical terms, the frequencies of separation between all combinations of the different factors in a group are largely a *function* of the distance apart of these factors in a linear figure.

It will now be desirable to consider these same facts from another angle. As it is possible to represent the linkages between *any three* factors of a group in terms of their distances on a linear diagram, it follows that *all* the factors of a group together can be represented in one linear diagram. Suppose that such a diagram has been made, and that the order of the factors in it is ABCDEFG. Now, as has just been explained, since per cent. AC nearly equals per cents. AB plus BC, it must follow that a separation between A and B rarely coincides with one between B and C; the same fact may also be expressed by saying that when A and B separate, C stays with B rather than with A. Similar relations, of course, hold for the other factors, too; thus D also stays with B and C when A and B separate, but it stays with C when B and C separate. The linkage of D with B, then, is only due to its linkage with C, for, although it usually stays with B, it very rarely stays with it except when C does. Thus D is linked to B only through C, and to A only through B. Similarly, all the other factors also are linked together in a chain, each to the one on either side: just as D is linked on the one hand to E, and on the other hand to C, but not to any other factors except through one of these, so C is linked on the one hand to D, on the other hand to B, but is linked to E only through D, and to A only through B, etc.; moreover, all the factors are linked to the others in the same order. Separation of factors in such a group accordingly means the breaking of the chain at just one or two points, for it has been pointed out that when B and C separate, A and

B rarely separate coincidentally, but usually remain together, and C, D, E, etc., all remain together also, separating in a body from A and B. In other words, the factors are not interchanged singly, but stay together in sections, according to their positions on the diagram, and whole sections are exchanged at once.

It may be objected that these conclusions are in many cases based on linkage values obtained in different experiments; that it is unwarranted to conclude, for instance, that when C and D separate, E remains with D, simply from the fact that in one experiment the frequency of separation between C and D had the value m per cent., in a second experiment DE was n, and in a third experiment CE was m + n, for this conclusion would only be true on the supposition that in all three experiments each factor had the same frequency of separation with each of the others as in the particular experiment where that frequency was determined. The answer is that numerous experiments have been performed in which three pairs of factors (or more) could be followed at the same time, and these experiments have given results precisely the same in kind, although more accurate than the preceding. But in experiments of the latter type, the coincidence of the various separations and non-separations does not have to be calculated out as in the case above, but is given directly by the results. Thus in a hybrid which has received ABC from one parent and the allelomorphs abc from the other, gametes in which coincident separation between B and A and between B and C has occurred will be distinguishable by having either the composition aBc or the composition AbC (see Fig. 3), and the number of such offspring can thus be directly counted instead of it being necessary to calculate them from the relations between separation values for A and B, B and C, and A and C. And in the experiment of the author's given in Section V, where the inheritance of a large number of factors is followed simultaneously, the results show directly and graphically that

the factors, as arranged in line in order of their linkage, are exchanged in whole sections at a time.

In the first section, evidence was presented, showing that groups of factors are connected with particular chromosomes, and segregate with them at the maturation divisions; this was in fact *proved* to be true in the case of sex-linked factors, which are found always to segregate with the X-chromosome during spermatocyte divisions. Yet it was conceivable that the factors were not actually *in* the chromosomes, but rather tied to them by some obscure connection (chemical, physical or metaphysical), although the fact that the relative sizes of the groups correspond to the lengths of the chromosomes might be taken as evidence against such a view. On that view, a separation of linked factors would be considered not a physical interchange between the chromosomes themselves, but a transference, by a factor, of its invisible bond, from one chromosome to the homologous one. But Sturtevant's evidence just presented shows that however one may have conceived, *a priori,* the chemical attraction or physical connection that makes linked factors tend to segregate to the same pole in the maturation divisions—this connection binds them in a *linear manner,* one after another, in a chain. This unique result, then, constitutes specific evidence that the factors are actually in the chromosomes, in an order which can be determined by their linkage relations, and that the separation of linked factors is consequently a real interchange between parts of the chromosomes themselves.[1]

[1] The fact of linear linkage does not connote that frequency of crossing-over is necessarily entirely dependent upon distance, for it is still possible to escape the conclusion that crossing-over occurs equally often in all parts of the chromosome, by assuming that coincidence of separations A–B and B–C usually occurs with not very different frequency from coincidence of separations G–H and H–I, even if different actual lengths are involved, provided the frequencies of separation are the same in the two cases. And on either way of explaining the results, the factors must be linked in line in the chromosomes in the same order as on the diagram. In fact, no matter how great the differences in frequency of crossing-over in different parts of the chromosome might be, the linkage order of the factors would still be the same as their real order so long as coincident crossing-over in any two regions did not occur as often as single crossing-over in either region.

Furthermore, admitting this conclusion that the linkage diagrams really represent the chromosomes, the fact that the factors are exchanged in sections proves that whole pieces of the chromosomes change places at once, as occurs in the process of "crossing-over" postulated by Jannsens, instead of small parts or factors in the chromosomes being separately exchanged. The idea that the interchange during synapsis may be a kind of exchange of separate particles from one container to another seems to have been held by a number of geneticists. On this view, the chromosomes might be considered as a sort of pod, containing the factors within them like so many beans; when the chromosomes synapse, the pods open towards each other, so that a factor in one might change places with a factor in the other. Conceivably—if we adopt this view—certain factors might be harder to dislodge than others, and so different frequencies of separation would exist between different factors. But such a mechanism of interchange would not result in a mode of linkage that may, in the sense explained above, be called linear, for separation of factor B from A would, on this mechanism, have no influence at all on whether or not C separated from A. This difficulty could be partially met by supposing that interchange of one factor in some way facilitates interchange of the neighboring factors, but the type of linkage which is actually found goes much further than this, and shows that the whole group of factors remains intact except at one or two points, interchange being in two or three entire sections. This can only mean, then, that interchange is a process of *crossing-over,* if it occurs by means of synapsis at all.

It might be claimed, however, that this interchange of whole sections of the chromosomes need not occur at synapsis, and therefore need not be of the nature of crossing-over at all. The only alternative to crossing-over, however, would be to suppose that, during the resting period of cells, the chromosomes might break up into pieces, and that then, in reuniting, a fragment of one chromosome

might become joined with a piece of the homologous chromosome instead of with a piece of the same chromosome. But on the fragmentation theory it must be supposed that the fragments reunite in exactly the original order, and, further, that the two homologous chromosomes break at precisely the same point before interchanging—otherwise one reformed chromosome would lack certain factors and the other would have too many; nevertheless, this point can not be a fixed point, as interchange may occur anywhere. Since interchange, when it occurs, usually takes place at one point only, it must also be assumed that the frequency of the recombination just described is so nicely regulated that in about half of the cases it has happened just once (and at one point in the chromosome) during the sum total of resting periods of all cells ancestral to any particular egg cell that shows interchange. For in about half the eggs a particular chromosome has exchanged in only two sections, and in very few have there been more than three points of interchange. Moreover, in the ancestry of the rest of the eggs, no interchange whatever can have occurred. Finally, the fallacy of the fragmentation idea becomes obvious when we consider that if interchange took place in the resting period of an embryonic cell, most of the eggs derived from this cell would show that particular recombination, and hence the individual in question would give an unusually large proportion of offspring of this sort. Thus different individuals of the same strain would differ greatly in their linkage values, there being scarcely any constancy at all. Since this is not true it would have to be assumed that interchange takes place only a short time before the maturation divisions, owing to some peculiarity in the chromosome processes occurring in the cells at this period. Thus we return again to the conclusion that interchange occurs during synapsis.

Further evidence that interchange occurs during synapsis is to be found in some results obtained with Bridges' "non-disjunctional" flies. Non-disjunctional females of

Drosophila contain, besides their two X-chromosomes, a Y-chromosome (owing to previous mitotic abnormalities). The presence of the extra homologous chromosome in some way causes the X's, in some of the oocytes, not to separate properly at the reduction division (presumably, this is because they did not pair with each other as usual, but one of them paired instead with the Y, leaving the other X free to go either to the opposite or to the same pole as the first X). Thus some of the eggs in which the above process has occurred come to contain two X-chromosomes, whereas normal eggs contain only one. Now, it is found that in those eggs which receive both X's, no interchange has taken place between them, whereas in the eggs containing one X, interchange has taken place about as often as usual. Hence interchange is connected with whether or not the Y allows the two X's to unite and separate properly, *i. e.*, interchange seems to be a result of the way in which chromosomes pair and separate during synapsis, and, as we have seen, if interchange occurs at this period, it must be by crossing-over.

B. The Correspondence between Separation Frequencies and Chromosome Lengths

In the present section still another possible test will be given of the conclusions arrived at by Morgan, that the factors are in line in the chromosomes, and that the order in which they lie determines in a general way the relative frequencies with which they separate from one another. And it has just been explained that evidence for these ideas is also evidence for crossing-over: that if the diagrams do represent the chromosomes and show the factors in their real order, then the facts of linkage demonstrate that, during synapsis, whole sections of the chromosomes change places at once, *i. e.*, cross-over.

The second test of the validity of the chromosome diagrams is as follows: If the order of the factors shown by their linkage relations, and represented in the diagrams, is their real order in the chromosomes, then it would be

possible, by adding together the frequencies of separation between all *adjoining* factors, to obtain the *total* frequency of crossing-over in the chromosome. This total frequency would be represented in the diagrams by the total length of the latter, since it is always the per cent. of separations between the most closely adjoining factors which is chosen to determine the number of units of length in any region of the diagram. Now, the total frequency of crossing-over in a chromosome ought, we should expect, to be determined by the length of that chromosome. Accordingly, we should expect to find differences between the total frequencies of interchange (or the diagram lengths) of the different groups of factors exactly paralleling the size differences existing between the chromosomes themselves. It will be seen, however, that such an expectation assumes also (1) that crossing-over occurs with equal frequency in all parts of a chromosome, and in equal parts of different chromosomes, and (2) that the factors available for working out the total frequency of interchange do not lie in any one limited region of the chromosome, but are more or less scattered, some of them lying near each end. A negative result from our test, then, might merely mean that one of these two assumptions was incorrect, and this would not disprove any essential point in the theory of crossing-over previously outlined. On the other hand, a positive result would seem to be too much of a coincidence to happen by mere chance, and so would seem to prove the correctness both of our main theory and of the two latter points.

In regard to the size relations existing among the chromosomes themselves, as determined by cytological observations, the work of Stevens (13), taken in connection with the later work of Metz (5), and of Bridges (2), shows that there are four pairs of chromosomes in *Drosophila:* a pair of moderately long sex chromosomes, two pairs of very long "autosomes," and one pair of minute "autosomes."

We may next consider the lengths of the genetic groups,

as determined by their "total frequencies of interchange." The length of the first, or sex-linked, group of factors has been found to be about 66 units; a unit, it will be recalled, is a section of the chromosome of such length that breakage occurs within it, on the average, one time in a hundred cases. The evidence then shows that, in a hundred cases, the first group breaks 66 *times*. This does not mean that it breaks in as many as 66 *cases* out of 100, for it may break two, or, very rarely, even three times, coincidently (at different points along the chromosome) in the same case ("double or triple crossing-over"). As previously explained, when two breaks thus occur coincidentally, the extremes of the chromosome come to lie on the same side, and so a factor at one end of the first group does not separate nearly 66 times in a hundred from a factor at the other end; owing to these coincident breaks it really separates in only about 45 per cent. of cases. The number 66 is consequently not obtained by merely determining the frequency of separation from each other of the two most frequently separating factors, but, as mentioned above, it must be derived by adding together the frequencies of all the smallest parts of the chain (frequencies of AB + BC + CD, etc.). In the case of the first group, the determination of this "total-length" has been accomplished by the combined efforts of a large number of people, although by the work of Morgan, Sturtevant and Bridges particularly.

Group II has a much greater length. It is probably over a hundred units long, and is certainly over 90. This result has been obtained principally by the work of Bridges and Sturtevant, although, as before, others have helped very materially. Mention must here be made of the fact that Sturtevant has discovered in this group specific mutant factors which, when *heterozygous*, lower the frequency of separation in certain regions of the group very much, although the order in which the factors are linked is not changed (16). The variation certainly proves, however, that (if the groups represent the chromosomes)

then, under certain special conditions of heterozygosis, different regions of the same chromosome may differ in regard to the frequency of crossing-over within them, for different regions were not affected in the same way by these factors; it also shows that equal lengths of different chromosomes may have different frequencies of crossing-over, for these factors affected only group II appreciably.

In group III, crosses involving several combinations of different factors have been made by Sturtevant, Bridges and Dexter, but the order of none of the factors has until recently been worked out by them nor has any consistent general scheme been attempted. The information has, in fact, not been adequate for this purpose, and much confusion has also arisen on account of the great linkage variation in this group, which seemed to occur very frequently. Sturtevant, who, as stated in section I, discovered the first case of linkage in the third group—namely, that between pink and ebony—had determined the initial positions of these factors, placing them at about 4 units apart, and next Bridges, who had found kidney (eye), had determined its position at about 15 units from pink, though he did not determine the relation between kidney and ebony. As a matter of fact, however, the kidney determination had been made with flies in which there was a greater frequency of crossing-over than in the experiments of Sturtevant, and, as will appear later, in any given experiment kidney is really nearer to pink than is ebony. From time to time after this other mutants were discovered (peach, Bridges, May, 1913; sepia, Wallace, May, 1913; spineless, Bridges, May, 1913; deformed eye, E. Cattell, 1913; band, Morgan, 1913; rough, Muller, June, 1913; sooty, Sturtevant, Oct. 1913; spread, Dexter, Nov. 1913; dichæte, Bridges, July, 1915), and the fact that these mutants were members of the third chromosome group was determined (peach, sepia, spineless, band and dichæte by Bridges; deformed by Cattell; rough by Muller; and sooty by Sturtevant). The author mean-

while undertook experiments with a view to determining the order of these factors, their frequencies of separation, and the manner in which these frequencies vary, and also sought to correlate with the results the data previously obtained.

It has developed from this work that group III is of the same "order of magnitude" as the first and second. This is the result required by the cytological facts. To complete the parallel, it should be found that the third group is longer than the first and, in fact, of just about the same length as the second group. Whether this is true can not yet be stated definitely, but the results indicate that it is. It is certain that the length of the group of factors dealt with is at least 55, but another estimate, which, for reasons given below, would seem more probable, gives the length as over 100. It should also be borne in mind that not as many factors have as yet been worked with in this group as in the other two, and it may well be that other factors will be found to lie beyond any of the twelve which have so far been approximately "placed." Thus, even if 55 should be the normal value for the factors *dealt with*, the whole group may very well be considerably longer. In the first and second groups, factors lying well beyond all the others were discovered after the positions of more than a dozen had already been determined.

The reason for the uncertainty in regard to the total frequency of separation among those factors which have been worked with is to be found in the linkage variation. Sturtevant had discovered that certain races, containing the mutant factor for ebony body color, gave extremely low frequencies of separation; that is, ebony flies, when crossed to those with pink eyes (pink is also in group III), gave a hybrid in whose germ cells very little recombination between pink and ebony occurred. Other races (*e. g.*, those containing sooty, an allelomorph of ebony), when crossed to pink, gave higher values. He therefore concluded that the ebony flies contain a factor (let us call

it C) which reduces the frequency of separation, and which is dominant, since it produces an effect in the hybrid. I have found that two other races of flies, one having the factor for spread wings (also in group III), and the other showing no "visible" mutant factors, also contain C, as they behave in the same way as ebony. However, the hybrids produced when these races are crossed with ebony give high frequencies of recombination again! This result shows that, as in group II, these races do not really contain a factor which normally reduces separation frequency, for, when both homologous groups of an individual contain the factor C—*i. e.*, when it is homozygous—the frequency of separation is high again. (This also explains an irregularity observed by Dexter, who obtained a high frequency of separation in a cross involving ebony flies.)

It happens, however, that these high separation frequencies obtained when C is homozygous are even higher than those occurring in crosses not involving C at all, and so presumably homozygous for its allelomorph, c. By analogy with Sturtevant's findings in the second group, this would mean that in most crosses hitherto made not involving C there has nevertheless been another factor heterozygous, which has a similar, but lesser, effect on the regions of the group studied. Some support for this interpretation is found in the fact that occasionally higher frequencies are obtained in these crosses not involving C, which appear to overstep the limits of chance variation. The evidence thus far secured on groups II and III points to the conclusion that the highest frequency obtained is that which should be regarded as the normal value, and that very marked departures from this, which affect only a particular group, are generally due to heterozygosis in special factors of that group. If it should be found that marked differences affecting the total frequencies of particular groups do occur, in cases where the flies are homozygous for whatever factors influencing linkage they may contain, we might naturally expect that

such variations would have gradually accumulated in the course of evolution, until no correspondence remained between the relative lengths of the chromosomes and the total separation frequencies. But the parallel which does exist between the observed chromosome lengths and the usual (homozygous) total frequencies, would seem too close to be meaningless, and so we should be led to believe that for some reason marked variations in the frequencies of particular groups, even though they may be possible, do not generally persist; in other words, the frequencies seem usually to stay at least roughly proportional to the actual chromosome lengths, and to furnish another verification of the theory of crossing-over. Further evidence of this will be met with when we consider group IV.

As the data whereby the positions of the factors and the total frequency of separation have been determined in group III, have not hitherto been published, it may be of interest to present some of them here. In order to obtain data on as many combinations of factors as possible in the same cross, so that the linkage values between the different factors would be comparable, I have endeavored to make up, by cross-breeding, stocks containing six or seven mutant factors in group III at the same time.

Since on account of the baffling linkage variation, the order of these factors could not well be determined by combining the results of separate experiments each of which dealt with only two factors at a time, it required a great many trial matings before such multiple stocks could be made up, as of course the crosses have to be made in a certain precise order, to secure a combination of many linked factors. To obtain stock ABC, for example, it would not suffice to make up AC and then mate it to B, for it would then require two coincident recombinations (which might never occur) to secure ABC. Moreover, as a first step it had been decided to get combinations of ebony with various factors, and very much time was lost in this attempt, as it was not then known that

when ebony is crossed to most other stocks recombination of the factors is nearly impossible. A stock has finally been obtained, however, combining the following characters belonging to group III: sepia eye color, dichæte (bristles, and wing), pink eye color, spineless body, kidney eye, sooty body color, and rough eye. Data have not yet been secured with this final stock, but the following experiment, in which most of these factors were involved, may be regarded as typical of crosses not involving factor "C," and consequently giving moderately high frequencies of separation. Hybrid females from a cross of sepia flies with flies containing dichæte, spineless, kidney, sooty, and rough, were backcrossed to the quintuple recessive stock—sepia, spineless, kidney, sooty, rough (dichæte being a dominant). The count of offspring is shown below. The classification as regards kidney has not been given, as this character can not be distinguished with certainty in eyes which are also rough.

No Separation

se	dic sps so r
131	109

Separation Occurring at a Single Point

1. Between positions of se and dic		2. Between dic and sps		3. Between sps and so		4. Between so and r	
se dic sps so r	normal	se sps so r	dic	se so r	sps dic	se r	sps dic so
9	16	20	15	23	19	40	28

Separations Occurring Coincidently at Two Points

1; 2. Between se and dic; dic and sps		1; 3. Between se and dic; sps and so		1; 4. Between se and dic; so and r	
se dic	sps so r	se dic sps	so r	se dic sps so	r
1	2	1	2	3	5

2; 3. Between dic and sps; sps and so		2; 4. Between dic and sps; so and r		3; 4. Between sps and so; so and r	
se sps	dic so r	se sps so	dic r	se so	dic sps r
0	0	2	3	1	1

In addition, 1 sooty spineless fly appeared, which must have resulted from a separation at three points coincidently ("triple crossing-over"), namely, between dic and sps, sps and so, so and r.

The above classification of the flies, in respect to where separation of factors occurred, is based on the assumption that the factors are linked in the order: se-dic-sps-so-r, as on any other arrangement the above results would show many more coincident separations between certain factors, than single separations. The reader may convince himself of this by working out the numbers of the different kinds of separations on any other scheme. We may say, then, that the above results prove that the factors are linked in the order just given. Turning to the individual separation frequencies, it will be seen that se and dic separated 25 times when there was no other point of separation, and 14 times when there was a coincident separation, *i. e.*, 39 times in all. As there was a total of 432 flies this means that these factors separated in 9 per cent. of cases, *i. e.*, are 9 units apart. In a similar way the results show that the distance between dic and sps is 10, between sps and so is 11, and between so and r 19.5, giving a total distance between se and r of $9 + 10 + 11 + 19.5 = 49.5$, which agrees well with the value 55, obtained by combining all the records of crosses of this general sort.

Factors Involved	"Distance" Between Them	Number of Flies on which Result is Based
Sepia dichæte	9.7	624
Dichæte spineless	11.0	683
Sepia spineless	23.4	1,014
Spineless sooty	11.7	1,198
Sooty rough	19.6	1,097
Pink spineless	8.5	825
Pink kidney	11.1	963
Kidney sooty	9.6	885
Pink sooty	19.9	1,566
Deformed pink	3.0	166
Kidney band	8.4	237

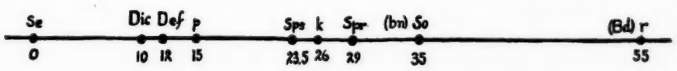

FIG. 5.

The following summary of "distances" between various factors of the third group (considered two at a time)

was obtained by averaging together the results of various experiments not involving C, in which I had followed the inheritance of both of the factors listed at the same time. Many of the data listed in separate lines are of course derived from the same experiment, as in most experiments more than two pairs of factors were followed. It should also be added that in one of the cases below (se sps), the distance was slightly lengthened to allow for coincident separations, the approximate proportion of which was known, but the actual number of which had not been determined in most of the crosses.

Having determined the order of the factors, these results may now be combined, in order to obtain a series of values based upon as many data as possible, and to construct a diagram of the group. The diagram so made is shown in Fig. 5. The numbers underneath the symbols of the factors represent the "distance" of the latter from sepia, which, as it lies at one end of the group, is used as a common point of reference. Although the distances shown will undoubtedly be subject to revision, the order of all the factors shown, except deformed, band, and beaded, is certain. Deformed (eye) is surely between sepia and pink, but it is not yet quite certain that it is to the right of dichæte; band (thorax) is near sooty, but on which side is not known; beaded (wing) is very near rough, but it has not been established whether it comes before or after it (a count of 50 flies showed no crossing-over between them). It was Sturtevant who first determined the position of beaded (found by Morgan, May '10) with reference to this series (to the right of sooty), and Bridges who first determined that dichæte lies between sepia and pink (about 4 to the left of pink). The data listed merely confirm these findings, so far as these two factors are concerned. And it may here be repeated that numerous other crosses of factors in this group have also been made by these investigators, although the crosses have not been of a sort to show the arrangement of the factors studied.

We may next consider the disposition of the factors of group III in a diagram based upon data from flies heterozygous for C. The separation frequencies which I have obtained are given below:

Factors	Per Cent. of Separations	Number of Flies
Sepia spineless	20.9	527
Spineless kidney	0.0	527
Pink kidney	1.5	868
Kidney sooty (or ebony)	0.2	674
Sooty (or ebony) rough	0.0	843
Kidney rough	0.1	1,211

A diagram based upon these data would show sepia at 0, pink at 19.5, spineless and kidney at 20.9, sooty and rough at 30, and the total length would thus be 30. The tenth of a unit of distance between kidney and sooty is based upon one fly, in which separation had taken place between these factors. Tests of the fly (which was a sooty rough, resulting from a backcross of a female containing p sps k so r from one parent and spread C from the other) showed that the factor C had remained with spread, and that no recombination had taken place between the positions of spread and sooty. This one fly, therefore, proved that both spread and C were to the right of kidney. The factor C is thus seen to lie right in the heart of the region where it exerts its maximum effect, as Sturtevant has also found in the case of the similar factors in group II.

Sturtevant has obtained slightly higher frequencies of separation between pink and ebony in some of his crosses heterozygous for C. The lower value here recorded may then be due to the flies being heterozygous for another factor besides C which disturbs separation frequency, and which is also met with in the crosses not involving C.

The following values have been obtained in crosses in which the factor C was homozygous:

Factors	Per Cent. of Separations	Number of Flies
Sepia pink	27.2	136
Pink ebony	48.0	290

Besides this, it is found that spread is about two thirds of the way between pink and ebony. Ebony, it will be remembered, is an allelomorph of sooty, and therefore occupies the same position. As no recombination has yet occurred between C and rough in flies heterozygous for C, it has not been possible to obtain these factors together and so, in crosses homozygous for C, the linkage of rough has not yet been discovered. The length of the group between sepia and ebony is 75 in these flies, as will be seen from the above data. Although these figures are based on a relatively small number of flies, the difference between this and the shorter value (35) found in flies not containing C is marked enough to be significant, especially since it occurred in various crosses of this sort. If the distance between sooty and rough is expanded in the same way, the group would have a length of much over 100. If, however, this distance is of the same length as in flies without C, the total length would be 95. The reasons have been given which incline us to the opinion that these values obtained in crosses homozygous for C may represent the "normal" figures for this group rather than those obtained in the experiments earlier cited. Further investigation of this point, however, is being undertaken.

Group IV corresponds with the pair of small chromosomes in that it contains so few factors. For this reason, the author, in his account of the inheritance of bent wing, in 1914, said:

> It also seems probable that when other mutations are discovered in the fourth group, the genes in which they occur will be found to be linked strongly to the gene for bent wings, since the fourth chromosome is probably the small one, and so any genes in it must lie near together.

One other mutant factor, "eyeless," has since been found, by Miss Hoge, to lie in this group. But although Miss Hoge has made numerous attempts (3) to combine eye-

less and bent, no recombinations between them have so far been obtainable. Group IV, therefore, forms a marked contrast to all the other groups as regards the frequency of separation within it, and this result is the more striking, not only because it shows that there is a group of factors corresponding in separation frequency to the pair of short chromosomes, but also because it happens that this group is the same one as that which had previously been identified with the pair of short chromosomes by reason of the fewness of the mutant factors discovered in it.

It is therefore evident, not only that the relative sizes of the chromosomes are in a general way like the separation frequencies of the groups, but also that where there is evidence from another source indicating in which chromosome a certain group lies, this is the very one to which the group corresponds by its total frequency of separation. It has been shown that this is true in the case of the fourth group. In the case of the first group, the sex-linked inheritance of the latter connects it with the X-chromosome, and since this is the moderately long chromosome, it is just this one with which group I would be identified by its frequency of separation. The other two groups, both of which are long—one certainly very long, and the other probably so—are thus left to correspond with the remaining chromosomes, both of which are very long and indistinguishable in appearance.

In the remainder of this article, therefore, the word "chromosome" will be used instead of "group" and "crossing-over" instead of "separation of linked factors."

(To be continued)

INDIVIDUAL DIFFERENCES AND FAMILY RESEMBLANCES IN ANIMAL BEHAVIOR

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IN experimental work on animal behavior, but little attention has been paid to individual differences, and practically none to family resemblances.[1] In studying the inheritance of conduct in man, experimental methods can not be used. Students of eugenics depend on observations difficult to verify. In the work here described an attempt has been made to apply the methods of genetics to the study of conduct. Such work was begun by Professor J. McKeen Cattell some fifteen years ago, but the results obtained by him and his students were not published, and the problem has been given to me.[2]

The plan of the experiment is to measure individual differences in behavior, to determine the extent to which the animal which departs from the average in one direction will depart in others, to measure the resemblances in families and in lines of descent, and to determine the degree to which kinds of conduct can be established in family lines by selection. It is evident that such a problem can be solved only by many years of work and with the facilities of a research institution. In the present paper there are described the individual differences and family resemblances of 90 mice, as determined by the time required to find their way through a maze. The same mice have been tested in other ways, and further experiments are now in progress with the F^5 and F^6 generations.

[1] Basset has recently published an article on "Habit Formation in a Strain of White Rats with Less than Normal Brain Weight." *Behavior Monograph Series*, No. 9, 1914. Macdowell in *Science* for November, 12, 1915, gives a brief abstract of work on "Parental Alcoholism and Mental Ability. A Comparative Study of Habit Formation in the White Rat."

[2] The greater part of the work presented in this paper was done at Columbia University, the results being used for a master's thesis.

A maze, designed by Professor Cattell, was used, the plan of which is shown in Fig. 1. The animal has in the

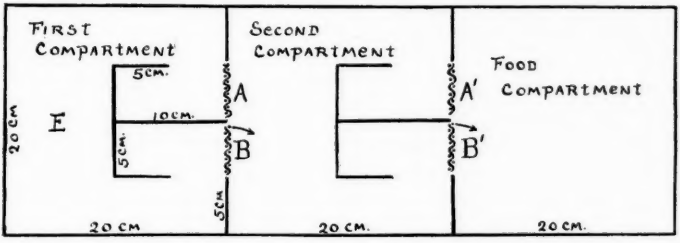

FIG. 1. Diagram of Maze. A and A' = closed wire gates; B and B' = open wire gates; E = entrance from above.

first compartment the alternative between two gates, one of which can be pushed open while the other is locked, and then it has the same alternative in the second compartment. When it takes the correct way in both compartments, it finds itself in the food compartment. The path that the animal must follow can be altered by changing the gates which are locked. "Unit construction" is used in the dimensions, which are adjusted to the size of the animal, and in the fact that any desired number of standard units can be added.

Preliminary tests were made with albino rats, but these were given up for mice, which are more active and more easily handled. The mice were given one trial each day, and were tested at as nearly the same time as possible. Light was found to play but a minor rôle in the tests, daylight and artificial light serving equally well. At the outset the age of the mice when first tested was not always known, but later when the various litters were obtained the young mice were tested at or about four weeks old.

The mice were rewarded for a successful trial by a mixed diet of milk, bread, oatmeal and sometimes meat. They always had a little dry bread in their cages. Besides satisfying their hunger, the mice had the additional reward of a place for exercise and the companionship of the mice that had just been tested. The order of the tests was

varied day by day. In case the way through the maze was not found in 360 sec. the animal was removed and tested again the following day. 360 sec. is thus the maximum record for a single trial.

Seventeen trials were made with each individual. This was a desirable number for two reasons: first, because this number was sufficient for the average mouse to learn the maze, and secondly, because the seventeen trials could be divided into three somewhat homogeneous groups. The first two trials are largely affected by chance, so, although given here for completeness, they are not averaged in the final ratings for each individual. The second group of five trials represents the period of more rapid learning, the third group of ten trials the results when the learning is slow or completed. In this paper the averages of the last fifteen trials are used as the index of performance. For some purposes the last ten or the last five trials might be preferable. The rate of learning as determined by the relation between the first and last groups may also prove to be of value.

In addition to the time, the number of errors, *i. e.*, the number of cases in which the mouse tried to go through the locked gate, is given in the tables, as this is a measure of the activity of the animal. With only a few exceptions, however, the error and time curves correspond. Consideration of the correlation between error and time, and between performances at the beginning and the close of the trials is postponed until data can be given for a larger number of individuals and the records for other kinds of behavior.

In Tables I to V are given the complete records of the 90 mice tested, grouped in families as described below. The average time is 44 sec. per trial for the last fifteen trials. The distribution of the individuals is shown in Fig. 2. In 41 cases the time was under 20 sec., in 19 cases between 20 and 40 sec., in the remaining 30 cases between 40 and 200 sec. None of the mice failed to learn the maze.

When the experiment started, several colored mice—chocolate, agouti, gray, black and yellow—were tested,

TABLE I

COMPLETE TIME AND ERROR RECORDS FOR THE YELLOW FAMILY

No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average	No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average
20Y♀	360	228	58	115	1.6	38Y♂	360	277	98	157	3.6
21W♂	247	41	11	21	.2	39Y♂	360	143	25	64	2.3
22W♂	234	28	14	19	.4	40Y♂	360	47	9	21	.8
23AG♂	280	43	6	19	.5	41Y♀	210	20	8	12	.5
24AG♂	182	47	8	21	.9	57Y♂	360	171	109	130	3.7
25AGW♀	177	136	26	63	1.7	58Y♂	357	130	51	77	2.4
26Y♂	360	206	172	183	3.7	59Y♂	360	275	98	156	3.3
27Y♀	201	10	14	13	.5						

In the first column is given the catalogue number, color and sex of the animals. In the second are the time averages (in seconds) for the first two trials; in the third, for the next five trials; in the fourth, the last ten trials, and in the fifth column the average of the two preceding columns. The error average for the last 15 trials is given in the last row of figures. This order is followed in all the subsequent tables.

One day's record has been omitted for mice Nos. 27, 28, 29 and 31 because the poor records for that day were obviously due to a constant error, on account of traveling, etc. These are the only cases where such a condition has occurred.

TABLE II

COMPLETE RECORDS FOR THE WHITE FAMILY

No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average	No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average
12W♂	360	91	56	67	1.9	103W♂	108	5	10	8	.5
13W♀	100	159	37	91	1.4	104W♂	174	12	13	12	1.0
15W♀	316	26	17	21	.4	105W♀	99	12	11	11	.8
48W♂	156	16	7	10	.5	106W♀	284	22	12	15	.9
49W♀	185	75	25	42	1.9	109W♂	101	69	8	28	.9
50W♀	246	25	18	20	.7	110W♂	93	11	7	8	.4
51W♀	56	13	7	9	.5	111W♂	67	13	12	12	1.0
52W♀	169	12	10	11	.9	112W♂	151	33	8	16	.9
53W♀	196	77	34	48	1.7	113W♂	88	11	7	8	.7
65W♀	285	87	8	35	.9	114W♀	75	13	5	8	.4
66W♂	360	306	17	113	1.2	115W♀	70	13	11	12	1.0
67W♀	360	173	25	75	1.7	116W♂	183	13	8	10	.7
76W♀	222	58	17	31	.9	117W♂	318	11	4	7	.5
77W♂	317	162	20	68	1.0	118W♂	81	14	10	12	1.0
78W♂	360	186	91	122	2.9	119W♂	115	40	9	20	1.1
71W♂	149	121	18	53	.9	120W♀	118	19	7	11	.5
72W♀	360	304	30	121	1.7	121W♀	64	17	9	12	.7
74W♀	89	29	21	24	1.2	122W♂	76	84	7	33	.7
86W♀	84	19	13	15	1.2	123W♀	66	39	29	32	2.2
87W♀	58	16	14	15	1.2	124W♀	25	23	10	14	.9
88W♀♀	86	14	7	9	.8	125W♂	189	15	7	9	.5
89W♂	110	16	10	12	.9	126W♂	90	19	9	12	1.0
91W	252	47	33	38	1.6	127W♀	72	22	11	15	.9

TABLE III

COMPLETE RECORDS OF A FAMILY CONSISTING MOSTLY OF YELLOW INDIVIDUALS

No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average	No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average
32Y♂	225	109	71	83	1.7	61Ch♂	360	202	30	87	1.0
33Y♂	154	186	42	90	.5	62YW♂	312	90	18	42	1.5
34Y♂	186	88	39	56	1.0	63YW♀	243	130	38	69	1.2
36Y♂	354	55	28	37	.9	64Y♀	360	182	113	136	2.3
37Y♀	137	20	16	17	1.2	68YW♀	112	71	65	67	2.0
54W♀	360	36	34	35	.7	69Y♂	177	41	9	19	.7
55Y♂	360	242	103	150	3.5	70Y♀	234	223	75	124	2.3
56Y♀	360	130	103	112	2.0						

TABLE IV

COMPLETE RECORDS OF A SMALL FAMILY SHOWING GOOD RECORDS

No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average	No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average
29W♀	229	9	8	8	1.3	45W♀	142	13	5	8	.5
30GR♂	58	43	33	36	1.0	46GR♂	141	9	4	6	.5
44W♀	297	16	7	10	.5	47B1♂	150	34	29	31	1.0

TABLE V

COMPLETE RECORDS OF THE UNRELATED INDIVIDUALS

No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average	No.	First 2 Trials	Next 5 Trials	Last 10 Trials	Last 15 Trials	Error Average
1Ch♂	212	48	11	23	1.0	5W♀	74	22	8	12	.6
2Y♀	285	213	103	140	5.1	28W♂	291	38	5	17	1.0
3Y♀	316	55	63	61	3.3	31GR♀	130	78	15	38	1.0
4W♂	77	18	14	16	.7	85W♂	131	14	9	11	.8

besides a large number of albinos, and among the yellow mice several made poor records. These mice were mated, and they and their offspring compose a group of 27 individuals, whose average time and error record is considerably in excess of the normal for the entire population.[3]

[3] This group of 27 mice was composed (see Tables I, III and V) of Nos. 20 and 26, and their seven offspring; No. 27, the sister of No. 26; a litter of five mice, Nos. 32, 33, 34, 36 and 37 and their ten offspring, and finally two unrelated yellow mice, Nos. 2 and 3, that were used at the beginning of the experiment. The 63 remaining mice of the white group bring the total to 90.

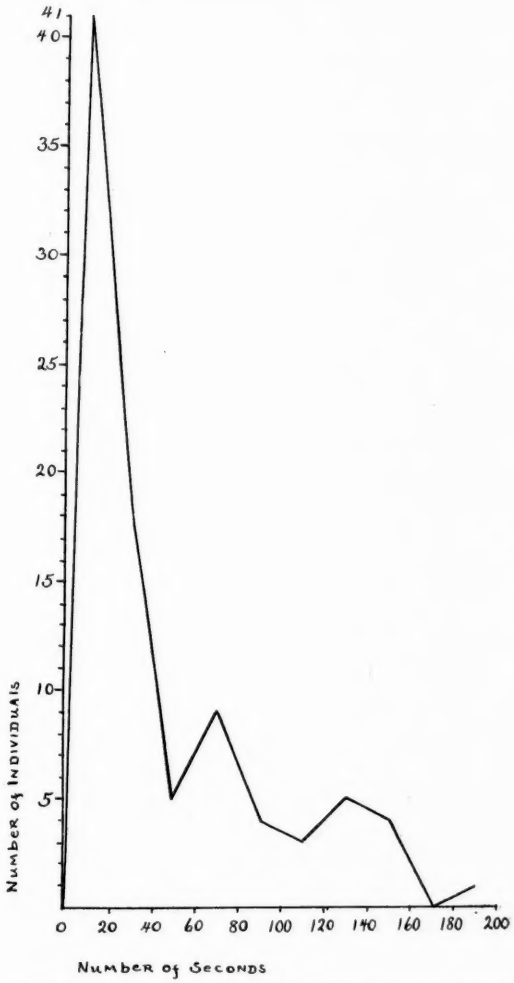

FIG. 2. Total distribution curve for 90 individuals for the last 15 trials.

The yellow group gave an average time of 83 ± 7.0 sec., and an average of 2.0 errors for the last 15 trials. The other mice gave an average time of 27.5 ± 2.0 sec. and .9 error per trial. The yellow mice were thus found to take,

on the average, at least three times as much time and to make twice as many errors as did the white mice. In Fig. 3, the distribution curves of both groups are given, the

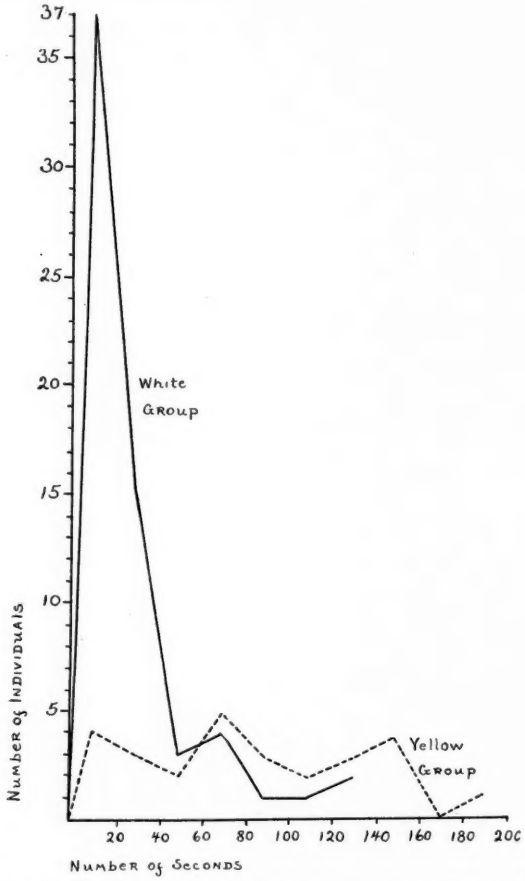

FIG. 3. 'Distribution curves of yellow and white groups for the last 15 trials.

yellow in a broken and the white in a solid line. The curve for the miscellaneous group is skewed, most of the individuals falling between 0 and 20 sec. The curve for the yellow family is nearly flat, there being about the same number of individuals in each time group.

Fig. 4 gives two average practise curves, one for the group of 63 white and colored mice, and the other for the group of 27 mice that are mostly yellow. The records of

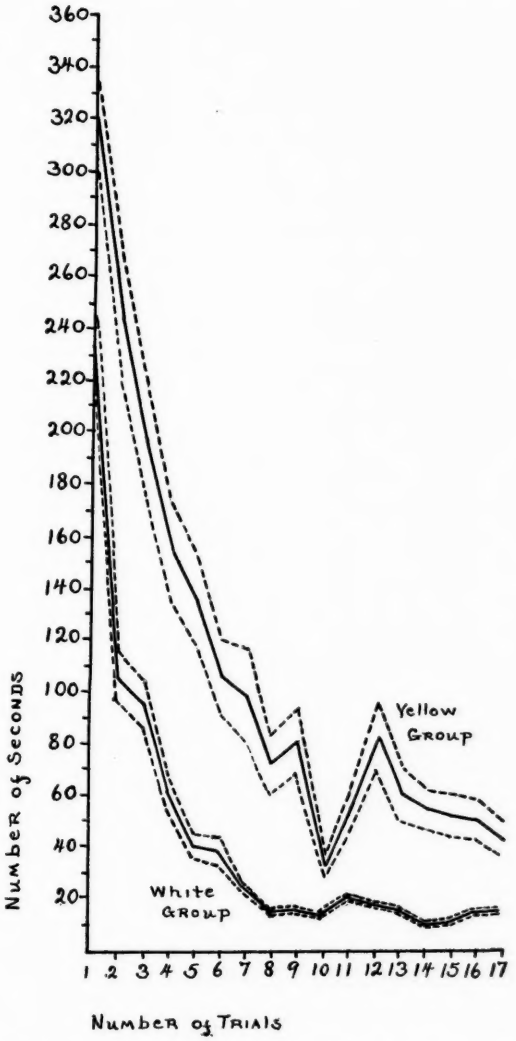

FIG. 4. Average record curves for yellow and white groups.

all the individuals for each successive trial were averaged, and the probable error calculated for each point on the curve. In accordance with a plan proposed by Professor Cattell, the limits of the probable error are shown by broken lines. The chances are even that with a greatly increased number of cases the time would have remained within these limits, and a nearly smooth curve can be drawn within them. A notable exception is the tenth trial with the yellow mice. At this point there is an unusually

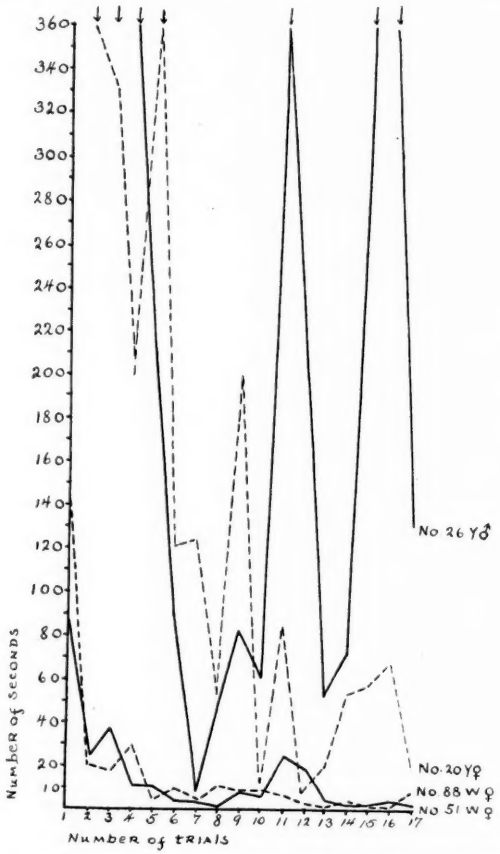

FIG. 5. Daily record curves for two white and two yellow mice.

large number of low records, more than the law of probability would warrant.

In Fig. 5 are given sample practise curves, showing the daily records for two white mice, Nos. 51 and 88, that learned the maze quickly, and for two yellow mice, Nos. 20 and 26, that were slow to learn. The arrows at the highest points indicate that the mouse did not pass through the maze. Thus No. 26 only got through on the fifth trial and failed in the eleventh, fifteenth and sixteenth trials.

The mean variation for the entire group of 90 mice was found to be 35.6. This means that any mouse picked at random from the mixed group would be likely to vary from the average by 35.6 seconds. In order to find whether mice of the same litter varied less than unrelated individuals, the mean variations for each of the 18 families was calculated, and these when weighted for size of family were found to be 20.2. The resemblance in behavior between mice belonging to the same litter was consequently nearly twice as great as between unrelated individuals. This corresponds to a coefficient of correlation in the neighborhood of 0.5 for brothers, as found by Pearson, Thorndike and others.

TABLE VI

AVERAGES FOR SEX DIFFERENCES

No.	Color	Sex	Average Last 15 Trials	Probable Error	Average Number of Errors
32	White, etc.	♂	27.69 Sec.	± 2.9	.9 per trial
31	White, etc.	♀	27.35 Sec.	± 2.9	1.0 "
15	Yellow, etc.	♂	90.0 Sec.	± 9.6	2.0 "
12	Yellow, etc.	♀	75.0 Sec.	±10.3	2.1 "

In Table VI, the males and females are grouped separately, and their average times and errors are given. In both groups of (mainly) white individuals, with 32 males and 31 females, and in the group of (mainly) yellow mice, with 15 males and 12 females, the times for the females are on the average slightly shorter, but the differences fall within the limits of the probable error and indicate that there are no sex differences in this kind of behavior.

We may now take up in more detail the family histories. Fig. 6 gives a graphic representation of matings, from

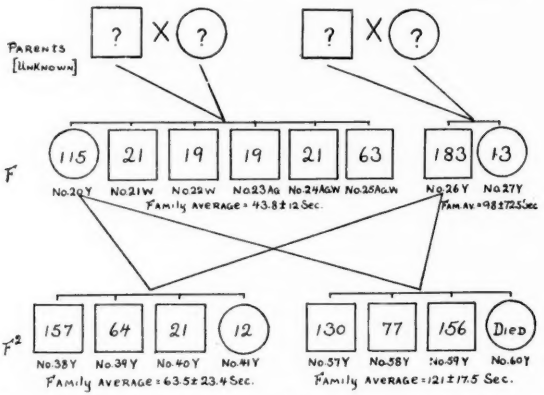

FIG. 6. Descent of yellow family. Squares denote males and circles females. The numbers within the circles and squares represent the average time taken for the last fifteen trials. The manner in which the yellow mice in these experiments have given an unusually large number of yellow offspring has been made the subject of another investigation from a mendelian standpoint.

which there were selected two mice, No. 20 Y♀ and No. 26 Y♂, which made unusually poor records, 115 and 183, respectively, though the other mice in the same litters had good records. The parentage of Nos. 20 and 26 was unknown; they were mated and gave two litters, each composed of three males and one female. Three mice in these two litters gave unusually slow records and made considerably more errors than normal. Two other mice gave poor records; two gave good records, while one died before it was tested. It is unfortunate that both females in these litters died before further offspring could be obtained. Table I gives the complete record of both time and error averages for these mice. It is a question whether or not the selection of parents having poor records tended to produce more than the normal number of offspring slow to learn. Further investigation can alone afford an answer.

The mice whose records are given in Table II are graphically represented in Figs. 7 and 8. They have been

carried down through the sixth generation, and are still being tested. As neither of the mice of the F^4 generation mated with No. 91, the only individual of the F^5 generation, No. 91 was mated successively with four unrelated

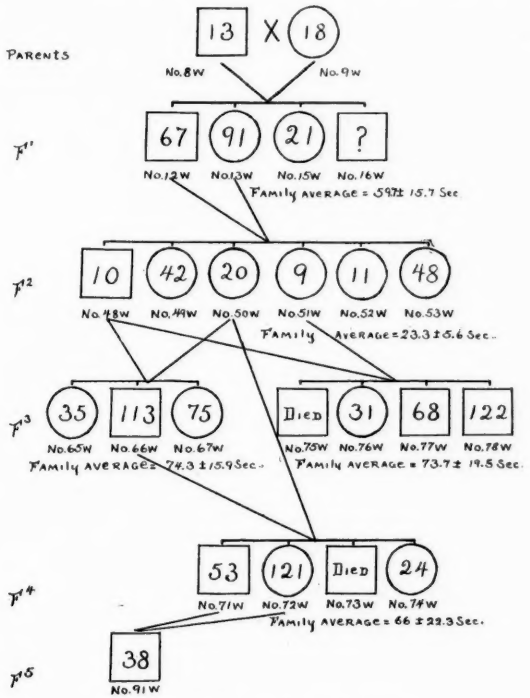
Parents
13 X 18
No. 8W
No. 9W
F1
67 91 21 ?
No. 12W No. 13W No. 15W No. 16W
Family average = 59.7± 15.7 Sec.
F2
10 42 20 9 11 48
No. 48W No. 49W No. 50W No. 51W No. 52W No. 53W
Family average = 23.3 ± 5.6 Sec.
F3
35 113 75 Died 31 68 122
No. 65W No. 66W No. 67W No. 75W No. 76W No. 77W No. 78W
Family average = 74.3 ± 15.9 Sec.
Family average = 73.7 ± 19.8 Sec.
F4
53 121 Died 24
No. 71W No. 72W No. 73W No. 74W
Family average = 66 ± 22.3 Sec.
F5
38
No. 91W

FIG. 7. Descent of a white family.

white females, Nos. 86, 87, 88 and 89. These females had been previously tested and found to give exceptionally good records as indicated in Table II. Twenty-three offspring resulted from these matings. Their records are remarkably uniform and the family averages are the lowest so far obtained. The records of these families are graphically represented in Fig. 8, and here only the continuation of the white family is given showing the F^5 and F^6 generations separately for each individual family. It

is hoped that future offspring may be obtained to continue this strain. The times for the fifteen trials do not always correspond with the times for the last ten trials.

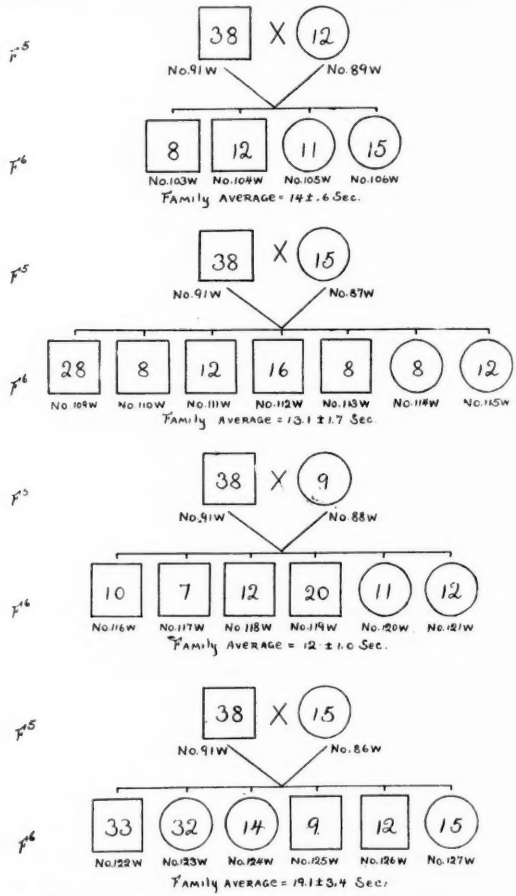

FIG. 8. Continuation of white family. No. 91 mated with four females.

Thus No. 66 has for the fifteen trials an average time of 113 sec., but in the last ten trials reduced the time to 17 sec. The capacity of the mice can only be finally determined after the same individual has been tested by different methods.

Another family, mostly yellow, was derived from a yellow female and an unknown male, probably white. The F^1 from this mating gave a litter of six, Nos. 32 to 37 inclusive. The records of 5 of these (one died) are given in Table III and are graphically represented in Fig. 9. The

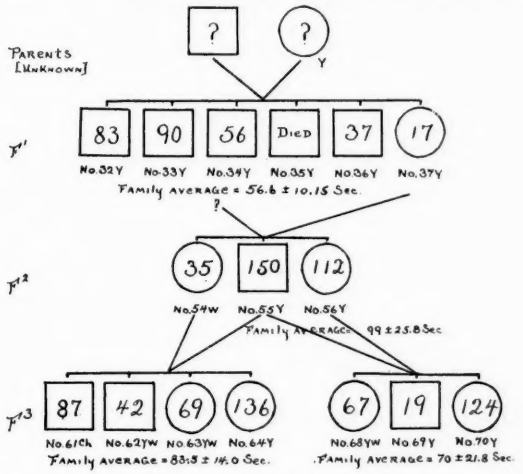

FIG. 9. Descent of a family of mice consisting mostly of yellow individuals.

only female of the litter (No. 37) mated but once, and it is not known with which brother. She bore in the F^2, two females and a male (Nos. 54, 55, 56). Both females of this generation were crossed with their brother and two litters resulted. No. 55×56 gave Nos. 68, 69 and 70 in the F^3, and No. 55×54 gave Nos. 61 to 64 inclusive. From a survey of the complete records of these mice, it is seen that although the F^2 and F^3 generations came from the female, No. 37 (which made the exceptionally low record of 17), still two of her young in the F^2 made poor records, and Nos. 61, 64 and 70 in the following generation did the same.

The records of a family of white and colored mice are given in Table IV and Fig. 10. The two parents and the four offspring all have good records. It is to be regretted that no further litters were obtained from this family.

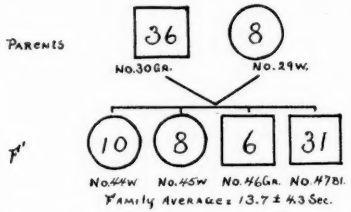

FIG. 10. Descent of a small family of mice showing good records.

In Table V are given the total records for the isolated cases, which complete all the individuals tested. Here again the relative inferiority of the yellow mice may be noted.

SUMMARY

1. Albino and colored mice can be used to advantage for laboratory work on animal behavior.
2. The type of maze used seems well adapted for this kind of work.
3. There is a marked difference in individual behavior.
4. There appears to be a resemblance among individuals of the same litter.
5. There appears to be a considerable difference among different strains.
6. The sex differences, if any, are very slight.

EVOLUTION OF THE CHIN

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University of California

In the Smithsonian Report for 1914 is an article by Louis Robinson, M.D., on "The Story of the Chin." Dr. Robinson in this article goes so far as to explain the presence of a chin in human beings as the result of the habit of articulate speech. Quite a different explanation is possible for the existence of this extraordinary feature of our anatomy. I should like to suggest some of the evidence which would seem to indicate that Dr. Robinson's ideas need rather careful review.

By chin is to be understood the projection or point on the under jaw, below the mouth (Fig. 1). The jaws of most vertebrates have no *projection* or prominence in this region.

It will therefore be recognized at the outset that the chin is a very "human" trait. It is a trait that distinguishes man from other living primates; even from his near relatives (compare Figs. 1 and 2). It even sets off

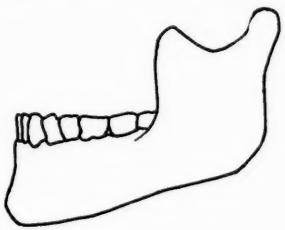

Fig. 1. Recent human lower jaw, showing the so-called "mental" or "chin" prominence.

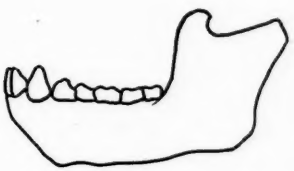

Fig. 2. Lower jaw of an orang, showing the absence of chin.

the man of to-day from the more ancient of his progenitors. The earlier fossil skeletons of man are quite chin-

less. The absence of this bony projection in the face is in fact one characteristic thing in our more or less ape-like forefathers (Figs. 3 and 4). The question is, how the "evolution" of this chin is to be explained.

Dr. Robinson's explanation seems to me to boil down to this: that man is, before all other creatures, a talker. In talking, the genio-glossus muscle is called upon to do the most work. This is a fan-shaped muscle which composes a large part of the under portion of the tongue, and is attached to the inner surface of the jaw just within

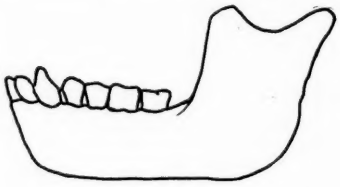

FIG. 3. The lower jaw of an ancient ancestor of man; the *"Eoanthropus dawsoni,"* an early Pleistocene form from Piltdown, Sussex (sketched from the restoration by Dawson and Woodward).

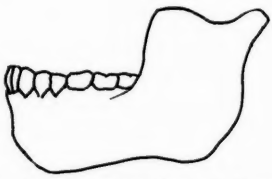

FIG. 4. The lower jaw of *Homo heidelbergensis,* a Pleistocene ancestor of recent man, found at Mauer near Heidelberg.

the chin. It is, according to Robinson, larger, more specialized in structure and more fully fasciculate in man than in the monkeys. The chin, then, says Robinson, is the point of origin for this elaborate muscle, which in a minute of conversation makes several hundred separate movements. The chin has crowded forward in its present conspicuous form as successive generations of men developed more adequate apparatus for speech. In other words, the chin developed because of the use and the consequent development of this one "talking-muscle."

It is only fair to remark that this is an old discussion. Walkhoff, in a series of papers, beginning with a volume edited by Selenka in 1901,[1] put forward the theory now rejuvenated by Robinson. The suggestion was critically reviewed by Fischer in a series of articles.[2] Since then the idea has appeared in a variety of journals.

[1] *Ausz. Biol. Centralbl.,* Volume 22.

[2] Especially *Anat. Anz.,* Volume 23 (1903); Volume 25 (1904).

It is only proper to say, further, that Robinson's various statements about the matter are hardly consistent. He states that the chin is, in origin, merely a buttress for the canine teeth; and he also believes it to be the result of sexual selection. Having accounted for it in these two ways, he throws in his remarks about the genio-glossus muscle for good measure. He closes by spending more discussion on the genial tubercles than on the chin itself. If the first of the statements to which reference has been made is correct, those animals which have large canines ought to be found with the best-developed chins. Quite the opposite is the case. Generally speaking, animals with very large canines, such as the baboons and others, are conspicuous for their very lack of chin. The author also makes certain sensational statements about the lower jaws of the "lower" races, that need full discussion; assuming in one place that uncivilized peoples have phonetically simple languages, an assumption which is startlingly contrary to the facts. His assumption that the genio-glossus muscle is the one prime factor in speech is not borne out by phoneticians, as he himself notes in one place (page 305). Aside from such minor points, all of which demand argument, I should like to point out what seem to my mind to be some of the more important reasons for considering his theory of the origin of the chin imperfect.

In the first place, if man's chin develops from his talking habit, all other animals, without exception, should lack chins altogether. None of them have a language, properly speaking. Robinson himself, to go no further, mentions other animals, notably the elephants, who do possess chins. The latter have it, as the saying is, to spare—much more than a human being has. Robinson points out quite correctly that talking and the chin develop together, as we observe man evolving through various types. This does not necessarily mean, as Robinson seems to assume, that talking produces the chin. On the contrary, the gluteus maximus muscle undergoes tremen-

dous development throughout the same period which brought in highly specialized language. No one has ever suggested, however, because it develops along with highly specialized language, that this muscle is concerned in speech. I should say that the proper method is to see whether there is any general tendency which would pro-

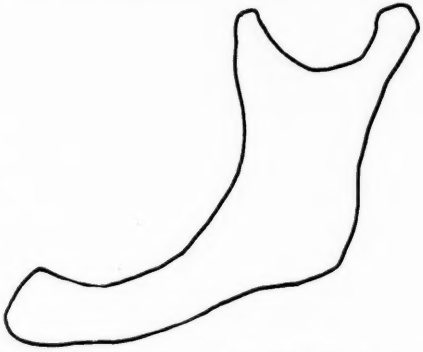

FIG. 5. The lower jaw of an aged person, showing the reabsorption of the alveolar border.

duce chins in the course of evolution, a tendency which would operate in the case of other animals, and also in the case of man and his forerunners. I think there is such a general principle, and a very simple one. I should be inclined to explain the chin, not as a by-product of speech, but as a result of a general reduction in the size of the jaw.

The man-like apes have very heavy chin-less jaws, which, in point of absence of chin, compare with the jaws of the great dogs or cats. Fossil man, too, exhibits, in the more ancient types, enormously large jaws. One general fact, then, in the evolution of modern man, has been a reduction in the size of this part of the body structure. This reduction went along with wider intelligence in the selection of food, and has perhaps been accelerated in man's case by the invention of cooking and other artificial treatment of food-substances. It is, then, a general tendency in the evolution of the human and related types. If we can not explain it, we may at least recognize

it. The next question is: if the jaw is in this way being reduced, should we naturally expect it to be equally reduced in all directions? There are reasons why we might anticipate that it would not.

If we consider especially the horizontal ramus of the jaw, the fact is striking that not all parts of it are equally permanent. The teeth themselves, and the upper border of the ramus, are temporary structures. In old age, the teeth are lost. The upper margin of the jaw itself is, in late life, reabsorbed (Fig. 5), which, with a corresponding loss in the upper jaw, produces the well-known nut-cracker appearance of the aged human face. Without attempting to dogmatize, I will go so far as to say that we might confidently expect that the region in the lower jaw which is lightest in structure, and the first to disappear in the individual, would be the part which would naturally respond first to the influence of external environment. Put in another way, the suggestion might be worded thus: We recognize as the important thing in the jaw the *teeth*. Hence, as smaller teeth became more appropriate through change of habit and environment, changes would first appear in these teeth themselves, and in the tissues which immediately support them. In fact, in the fossil "Heidelberg" jaw the teeth have been reduced faster than the jaw itself.[3] Granted that our ape ancestor had a jaw, it

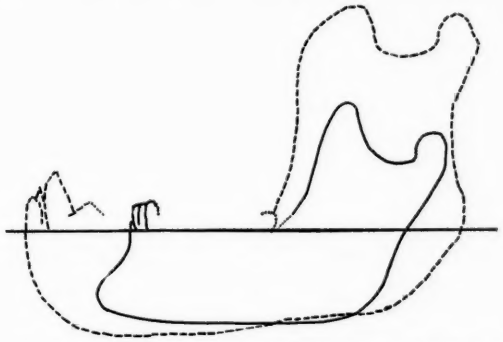

FIG. 6. Lower jaw of the gorilla (broken line), compared with the lower jaw of recent man (adapted from Schoetensack). If the recession in successive gorilla jaws were more rapid in the upper than in the lower border, a prominence would be produced as shown in the human jaw.

is to be expected, it seems to me, that during a general contraction in its size, the superior margin would retract more rapidly than the inferior. I am inclined to think that the chin is the persistent lower margin of our large ancestral jaw. This margin has become retracted more slowly than the upper margin, and therefore juts out into space (Fig. 6).

A difficulty immediately suggests itself. If a *human* chin results from reduction in the size of the jaw, wherever in different species of animals jaws have become reduced, we ought logically to find chins. One striking case can be cited in line with this suggestion. The case of the elephant suggests itself at once, and very clearly. We know that his jaw bones are the result of a remarkable retraction. The process is one of the most picturesque that we know about.[4] We duly find in the geologically recent elephants, and especially in the living species, a tremendous chin (Fig. 7). Whether still other

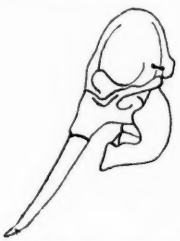

FIG. 7. Face of the Indian elephant (recent), showing the presence of a conspicuous chin which has resulted from reduction in the length of the jaw.

cases of chins resulting from retraction could, or could not, be cited, I do not know. I very strongly suspect, however, that a thorough knowledge of paleontology would put one in position to cite a considerable number, though possibly few cases would be so clear as that of the elephant. I can not resist the feeling that in some such process we have the explanation, not only of human chins, but the chins of other animals as well.

[3] A fact mentioned by MacCurdy in the Smithsonian Report for 1909 (page 570).

[4] Interestingly described by Sir Ray Lankester, "Extinct Animals."

HYBRIDS OF THE GENUS EPILOBIUM

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THAT hybridism and sterility are closely related has been long recognized in a general way, but it is only within the last few years that a systematic and comprehensive investigation, at least of the plant kingdom,

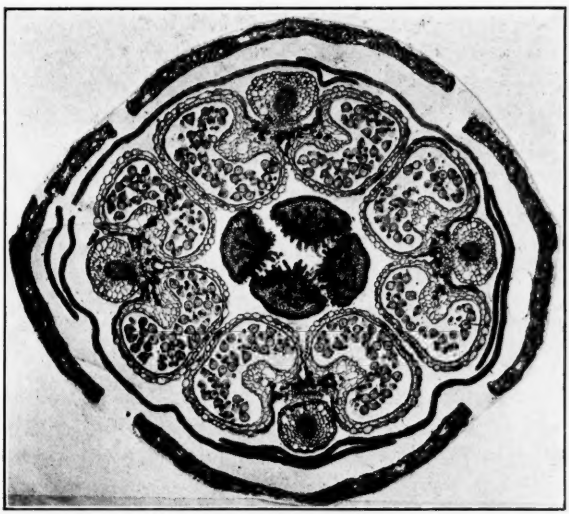


FIG. 1. Flower of *Chamænerion angustifolium*, Southern Ontario.

has been attempted. Professor Jeffrey and his students,[1] working on the flora of eastern North America, have

[1] Jeffrey, E. C., "The Mutation Myth," *Science*, N. S., 39: 488–491, 1914; "Spore Conditions in Hybrids and the Mutation Hypothesis of De Vries," *Bot. Gaz.*, Vol. LVIII, No. 4, Oct., 1914; "Some Fundamental Morphological Objections to the Mutation Theory of De Vries," AMER. NAT., 1915; Holden, R., "Anatomy as a Means of Diagnosis of Spontaneous Plant Hybrids," *Science*, N. S., 38: 932–933, 1913; "Anatomy of a Hybrid Equisetum," *Amer. Jour. of Bot.*, May, 1915.

demonstrated that the infertility of hybrids is due to the abnormal development of the gametic elements, particularly the pollen grains, and have shown that whenever the purity of a species is unquestionable, the spores are uniform, in both size and shape, while, conversely, the spores of hybrids are usually irregular, some appearing normal and others being shrunken and devoid of proto-

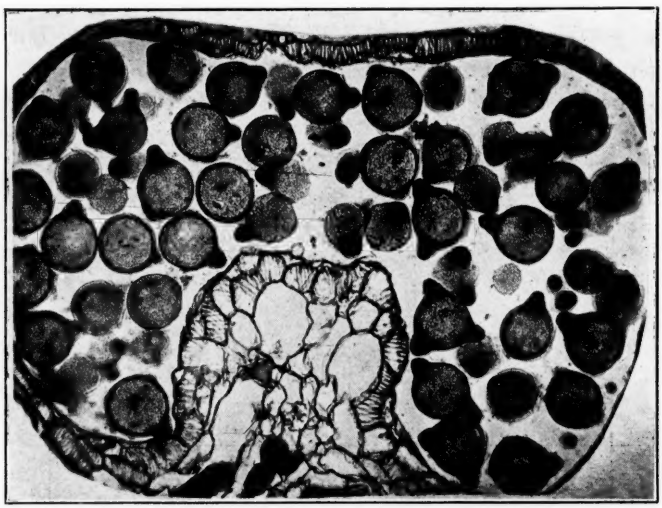


FIG. 2. Half of Anther of *C. angustifolium*, Southern Ontario.

plasm. During the past year the writer has extended these investigations to include a considerable number of English species. Many interesting cases have been encountered, which will be elucidated in detail on another occasion, but the conditions in the genus *Epilobium* are so diagrammatic and typical, that it seems advisable to describe them now.

This genus is divided into two sections, *Chamænerion* and *Epilobium* proper, the chief differences being that in the former the flowers are irregular and the spores not in tetrads, while in the latter the flowers are regular and the spores are persistent as tetrads. Both in eastern

North America and in England, the former section is represented only by *E. angustifolium* (L.), while the latter includes numerous species. Moreover, although the species of the *Epilobium* section are generally recognized to hybridize freely with one another, they do not hybridize with the *Chamænerion* section. Accordingly, one would expect to find only good pollen in the anthers of *E. angustifolium,* and a mixture of good and bad in all the others. Investigation of the North American forms showed that such was indeed the case, and photomicrographs illustrating these conditions were published.[2] When the writer came to examine English specimens, however, a different state of affairs was discovered. Abortive spores were found not only in *E. montanum, E. parviflorum* and *E. hirsutum,* as might have been an-

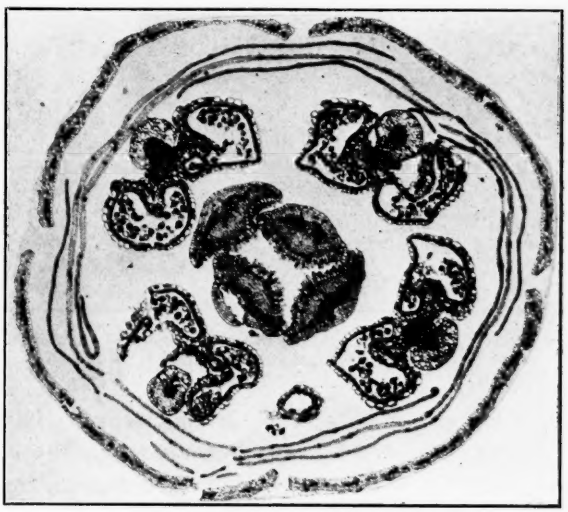


FIG. 3. Flower of *Chamænerion angustifolium* (Hardwick, England). Showing shrivelled anther.

ticipated, but also in *E. angustifolium. E. angustifolium* grows wild in only two localities in the vicinity of Cambridge, Hardwick and Gamlingay, but in specimens from

[2] *Loc. cit.*

both these places, as well as in others from the botanical gardens of Cambridge University, the same mixture of good and bad grains was found. These facts seemed to invalidate the conclusion that abortive spores are an invariable sign of hybridism, but, as has so often been the case in scientific matters, evidence which at first seems to discredit a given hypothesis, on further investigation is seen actually to corroborate that same hypothesis.

Reference to systematic works shows that there are two varieties of *E. angustifolium* growing in England, *E.*

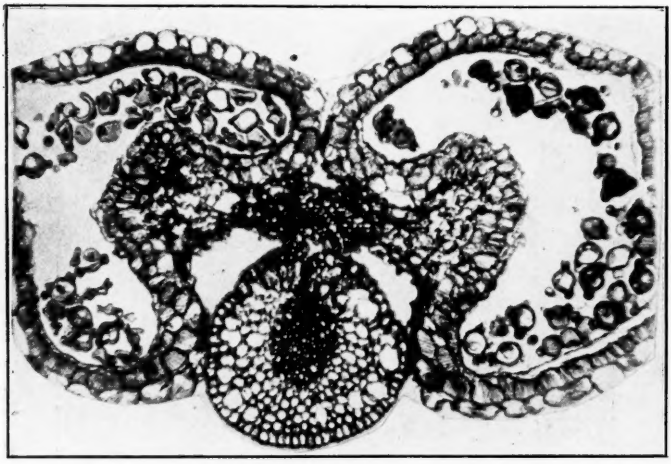


FIG. 4. Transverse section of *Chamænerion angustifolium*, showing abortive pollen. (Hardwick, England.)

macrocarpum (Steph.) and *E. brachycarpum* (Leight). There are a number of minor differences in the length of the stolons, shape of the leaves, flowers, etc., but the most definite is the relative length of capsule and pedicel. *E. macrocarpum*[3] grows sparingly but generally from Somerset and Hants. to Orkney, while *E. brachycarpum*, though cultivated commonly all over England, is found much more rarely in the wild condition, being recorded

[3] Boswell, Syme, "English Botany."

from Shropshire, N. Wales, Yorkshire, and even near Edinburgh. Through the kindness of Dr. Wilmott the writer was able to examine the spores of a considerable number of both these varieties from specimens in the herbarium of the British Museum, and in every case the anthers contained a mixture of normal and abortive grains.

We have here, then, a very interesting condition—wherever the two varieties of *E. angustifolium* are present, the spores are partially abortive—indicating the bar sinister; this state of affairs is found in England, and probably in Europe, Asia and western North America, where both varieties are known to coexist. Wherever, on the other hand, as in southeastern North America, there is but one variety, the spores are all normal. *Chamænerion,* therefore, instead of discrediting the value of abortive pollen grains as a test for hybridism, affords another instance of its value. It also suggests another question—how far apart genetically must individuals be before the spores begin to degenerate? Hitherto it has been assumed that only crosses between recognized species bring about that result, but in the case of *Epilobium,* the varietal difference appears sufficient. This, however, opens up the whole question of what is a species, and can not be entered upon here.

SHORTER ARTICLES AND DISCUSSION

CAN SELECTION CAUSE GENETIC CHANGE?

IT is almost a pleasure to have occasion for controversy with a fellow worker who shows himself so fair-minded and generous an opponent as does Dr. Pearl in the AMERICAN NATURALIST for February, 1916. He credits my investigations with greater merits than I have claimed or can claim for them. If they possess any superiority, it is not because they have been either better planned or better executed than Dr. Pearl's, but only because the material used was more favorable. In my experiments with rats I have simply undertaken a less difficult task than that undertaken by Dr. Pearl in relation to the fecundity of fowls. Pearl is right in supposing that I have no desire to convey the impression that his work is valueless. No one has greater admiration than I for the masterly way in which he has analyzed the fundamental problems of genetics and the thorough and systematic way in which he has attempted their solution. I regret only that he has courageously attacked so complex a problem before certain simpler and more elementary ones had been solved. I felicitate myself only on having been content with a less ambitious program.

I am pleased to learn too that we are so closely in agreement as regards the observational facts, that in reality it is only concerning the *interpretation* of results that our views seriously differ.

I am quite ready to grant that we are concerned with the same fundamental question, that of the possible quantitative change in a character under selection, that the methods which we have employed are substantially the same and that these methods are open to similar objections, that *random sampling* occurs in the rat experiments as well as in those with fowls, though it is involved in a further degree in the experiments with fowls because of limitations of age and sex. I am quite willing that Pearl should recall the statement "that phenotypic variation of the character fecundity in fowls, markedly transcends, in extent and degree, genotypic variation," and that he should substitute in its stead the statement that it "*may*" so transcend. I am even

more ready to concede the existence of genotypic variation in this character than Pearl has shown himself to be. And I have been reluctant to accept at its face value Pearl's statement that at the conclusion of his fecundity selection experiments he had *more* good winter layers than at the beginning, but none *better*. For in our selection experiments with rats it is very clear that when high-grade individuals grow common, a few individuals of *higher* grade are sure to put in an appearance. Genotypic variation seems to me to be of such wide occurrence that it is difficult to believe that it is ever wholly absent, that absolutely pure lines really exist. I quite agree with Pearl's conclusion that somatic character is not a sure index of genetic constitution and that it was therefore entirely logical and necessary for him to make progeny tests in order to classify his pullets genetically. To establish the point it is not necessary for him, as he observes, "to be fussily nasty" by citing page after page from my Mendelian writings. I had granted the point years before it was raised.

This brings us again to what Pearl considers "the most serious phase of Castle's attack, namely that in which he denies the validity of my conclusions respecting the inheritance of the character fecundity in fowls." Let it be made very clear at the outset *what* is attacked. Not the idea that fecundity is inherited. I think that I am even more ready than Pearl to admit that fecundity is a quantitatively variable character and that its various quantitative conditions are inherited. This is merely to state in another way that *genotypic* as well as *phenotypic* variations in fecundity occur. If they occur, it is possible to isolate them and thus to produce families characterized by them. The conclusion which I "attack" is this, that the observed variations in fecundity depend upon two and *only two* differential factors, both of which are Mendelian, one sex-linked and the other not sex-linked. Several possibilities are conceivable, which this conclusion does not include, as for example that *more* than two genetic factors are concerned in the variation, that one or other or both of the supposed factors are quantitatively variable and so capable of gradual change under selection. I am not advocating or defending any of these possibilities. I am merely attacking the conclusion outlined substantially as I understand Pearl to hold it. There are really several distinct points in this conclusion, some of which seem to be better grounded than others. If I were asked either to accept or to reject it *as a whole* (and Pearl's pub-

lished data leaves no alternative to this) I should reject it, and this decision would not be influenced by the consideration that Morgan, Doncaster, Johannsen and Plate accept it, because it accords with the conception of the pure-line which they have adopted. Authority does not count in science. Majorities do not decide what is true. If they did, Mendelism would have been false in 1868 and true in 1900. If Morgan and Johannsen should next week decide against the pure line idea, as Jennings has already done, what could the rest of us then do except change our minds too, if we base our scientific judgments on authority? Dr. Pearl, I am sure, would be the last to advocate such an idea.

I grant to Pearl the legitimacy of his method in attacking the problem of the inheritance of fecundity and the necessity of establishing arbitrary categories of winter egg production in which his birds are then classified. But I regret what seems to me to be the needless restriction of his published data to the contents of these categories. Pearl points out that I too have made use of arbitrary categories in dealing with the rat statistics, but I would call attention to this difference in our procedure. My categories, +1, +2, etc., are indeed arbitrary, but I have not limited the reader's information to their contents. I have published the data in such form that the reader may, if he chooses, form new categories with different inclusiveness, subdividing each category and then subdividing these again down to the lowest limit of observation which can be made with certainty. Pearl has not made it possible for us thus to deal with his data. We may take it or leave it, but we can not change it. We have no means of knowing how many pullets laid 1–10 eggs in their first winter, how many laid 11–20, or 21–30 eggs. In what particular are these "original records" which Pearl withholds "valuable" except as proof of the conclusions which he sees fit to base on them? If he decides, as announced, that the data are not to become public property until he has finished his own study of them, he is well within his rights, but what is the hurry about forcing the *conclusions* upon a waiting public? Would not the public be justified in deferring its decision as to the validity of those conclusions until data as well as conclusions are available?

Pearl seeks to offset his own sin of omission by charging a like offence upon me, maintaining that the scientific public withholds acceptance from my conclusions concerning the rat selection experiments solely because I have never presented my results "in

such form that any other interpretation of the data could by any chance be tested.'' If this statement is true, it is because of my inability to devise any other form in which to present the data. I have presented it in such form that the limits adopted for the categories of variation could be shifted at will and I am ready to be shown how its presentation can be further improved and simplified. Pearl suggests that my omission pertains to the individual pedigree of the rats, in which suggestion he echoes a thought of the Hagedoorns on which I have twice commented elsewhere, showing, I think, that the alleged defect does not exist, for the following reasons:

1. It is impossible for a colony of 33,000 rats to be produced from an original stock of less than a dozen animals, with constant breeding together of those which are alike in appearance and pedigree, and with continuous selection of extremes in two opposite directions, without the production of pedigrees which in the course of each selection experiment interlock generation after generation and finally become in large part identical with each other. This has been repeatedly verified in individual cases, but is incapable of a more generalized statement or of demonstration in generalized form. At least I am unable to devise such demonstration.

2. In a specific case described on pp. 20 and 21 (Castle and Phillips) a selection experiment was started with the hooded F_2 offspring of a single selected hooded and a single wild rat and this experiment was carried through the F_8 generation leading to the production of 804 young from rigidly selected, closely inbred descendants of a single pair. We showed (l. c., p. 21) that the progress of selection within this inbred family follows a remarkably close parallel, generation by generation, to the progress of selection in our plus series as a whole. Here there can be no question of a difference in pedigree among the selected animals. This is eliminated as a possible factor in the result. Can Pearl suggest any other possible factors capable of elimination? If so, I should be pleased to give attention to them.

I humbly beg pardon for having made the all too obvious suggestion that environmental conditions, and in particular size of flock, may affect average flock fecundity. And yet I find that Pearl himself elsewhere lays great stress on this point. My chief offense seems to lie in my failure to realize that he had already taken all possible precautions in this matter, and that he consid-

ered himself in a position to vouch for the uniformity of environmental conditions, not only in eight years of experiments which he had personally superintended, but also in nine previous years of experiments of which he had neither control nor information until they were completed and which were made sometimes in 50, sometimes in 100, and sometimes in 150 bird flocks. Are there not here some elements of uncertainty which at least condone the offense even if they do not excuse the question?

I am prepared to accept without question Pearl's statement that date of hatching can not possibly have had anything to do with the rise in average flock production which has occurred between 1908 and 1915, notwithstanding his own previous statements on the subject and the evidence which Phillips has produced that date of hatching of ducks affects their adult size. I am prepared to accept the view that this rise was due wholly to genetic changes, but I do not believe that Pearl or any one else is in a position to say to what agencies the decline previous to 1908 was due.

And now, with Pearl, I turn with pleasure to the general problem of selection and note that our differences are here rather verbal than real. They lie in that philosophic pitfall of *causation.*

Pearl can not conceive that selection may *cause* or *occasion* or *lead to* genetic change, though he can readily see how populations may change under its influence. Thus selection may increase the proportion of high-grade individuals but it can not, on his view, beyond a limited and fixed point, occasion the production of individuals of increased grade. With these views I squarely take issue, and I shall try to show that his view is a purely *a priori* view, while mine is based on both observation and experiment.

Pearl's reasoning throughout rests on the assumption that the potentiality of a germ cell can not change except by a *causeless* method, "mutation"; that no extraneous influences can change it. Experience teaches directly the contrary, indicating that germ-cells brought together in fertilization mutually *influence each other.* Let us consider for a moment Pearl's illustration. He supposes an organism to exist, A_{38}, which is producing gametes of the uniform value, a_{38}, and can not understand how such gametes uniting with each other can ever produce individuals of a higher value, say A_{39}. No more can I, if we accept his further

hypothesis that there is to be "no mixing of germ-plasms." But what justification have we for that further hypothesis? Experience furnishes none. On the contrary, I have shown in numerous specific cases that when unlike gametes are brought together in a zygote, they mutually influence each other; they partially blend, so that after their separation they are less different from each other than they were before. The pure-line advocates have adopted the procedure of dismissing such explanations as mystical, an easy way to dispose of troublesome ideas. But the stubborn fact remains to be accounted for that partial blending does occur (1) when polydactyl guinea-pigs are crossed with normals (Castle, 1906), (2) when long-haired guinea-pigs are crossed with short-haired ones (Castle and Forbes, 1906) and, (3) when spotted guinea-pigs or rats are crossed with those not spotted (MacCurdy and Castle, 1907). Davenport has furnished numerous instances of the same thing in poultry; indeed he has shown that "imperfection of dominance" and of segregation are the rule rather than the exception in Mendelian crosses in poultry. To assume that "there is no mixing of germ-plasms" is a contrary-to-fact assumption, whatever it may be in formal logic or scientific methodology.

Let us change slightly Pearl's hypothetical case. Let us suppose, as he does, that a gamete a_{38} has united in fertilization with another a_{38} gamete producing a soma, A_{38}. Now what sort of gametes may we expect such an individual to produce? Pearl says, in effect, nothing but a_{38} gametes, unless a genetic miracle occurs, a mutation, incapable of casual explanation. But we should hesitate to characterize as miraculous anything which occurs with regularity, and experience shows that this is what happens quite commonly, if not regularly, in such cases. The A_{38} individual produces gametes a *majority* of which have the value a_{38}, but a few of which have a higher value, a_{39}, and a few a lower value, a_{37}. For the correlation in value between soma and gamete is not absolute. It is in many cases close, but not invariable, as I think Dr. Pearl would admit. If it be granted for the sake of argument that gametic variation occurs, it is obvious that we have grounds for expecting somatic variation in the following generation. For an a_{39} gamete uniting with another gamete like itself may be expected to produce a zygote of value A_{39}. Pearl maintains that such an event is without "causation," is incapable of prediction and control, that all we can do is to

record its occurrence, a view I by no means share. But, it may be asked, *what control* can we exercise over the event? We can prevent or permit it at will. For observation shows that if we permit the individual to mate only with those of inferior value, we shall get no offspring of the highest grade. Thus $a_{38} + a_{36}$ produces commonly only A_{37}, rarely A_{38} and, we might say, never A_{39}. But if we permit the individual to mate with individuals of *equally* high grade (and this is what selection in a particular direction does) experience shows that a majority of the offspring will be of that same grade, but a *few* will be of higher grade. These few make possible further advances. Thus a_{39} makes possible the subsequent attainment of a_{40}. Whether this relationship involves "causation" or not is a question for the logicians and methodologists, of whom I am not one. As to the *fact* our rat experiments leave no doubt. In the light of such facts it seems to me that a view earlier held among biologists, that variability is one of the fundamental properties of organisms, comes nearer to the truth than this modern notion of the pure, unvarying line. This pure-line concept Pearl rightly characterizes as "one of the most useful working tools in the practical breeding of plants and animals that has ever appeared." Why useful? Because it has caused us to pause and take careful inventory of our facts, and to discard as rubbish many loosely held notions. But Pearl reminds us that not all the pure linist's facts are in one basket with Johannsen's beans, nor even in that other vanished basket with Jenning's paramecia. There are, he reminds us, "all the Svalöf oats and wheats to be reckoned with." True and they are mute witnesses to the cumulative effects of selection. For all agree that these pure lines of oats and wheats are the product of continuous self-fertilization. And what more than self-fertilization renders possible generation after generation the union of gamete with its like, the indispensable condition for progressive variation in a particular direction, as I have tried to show?

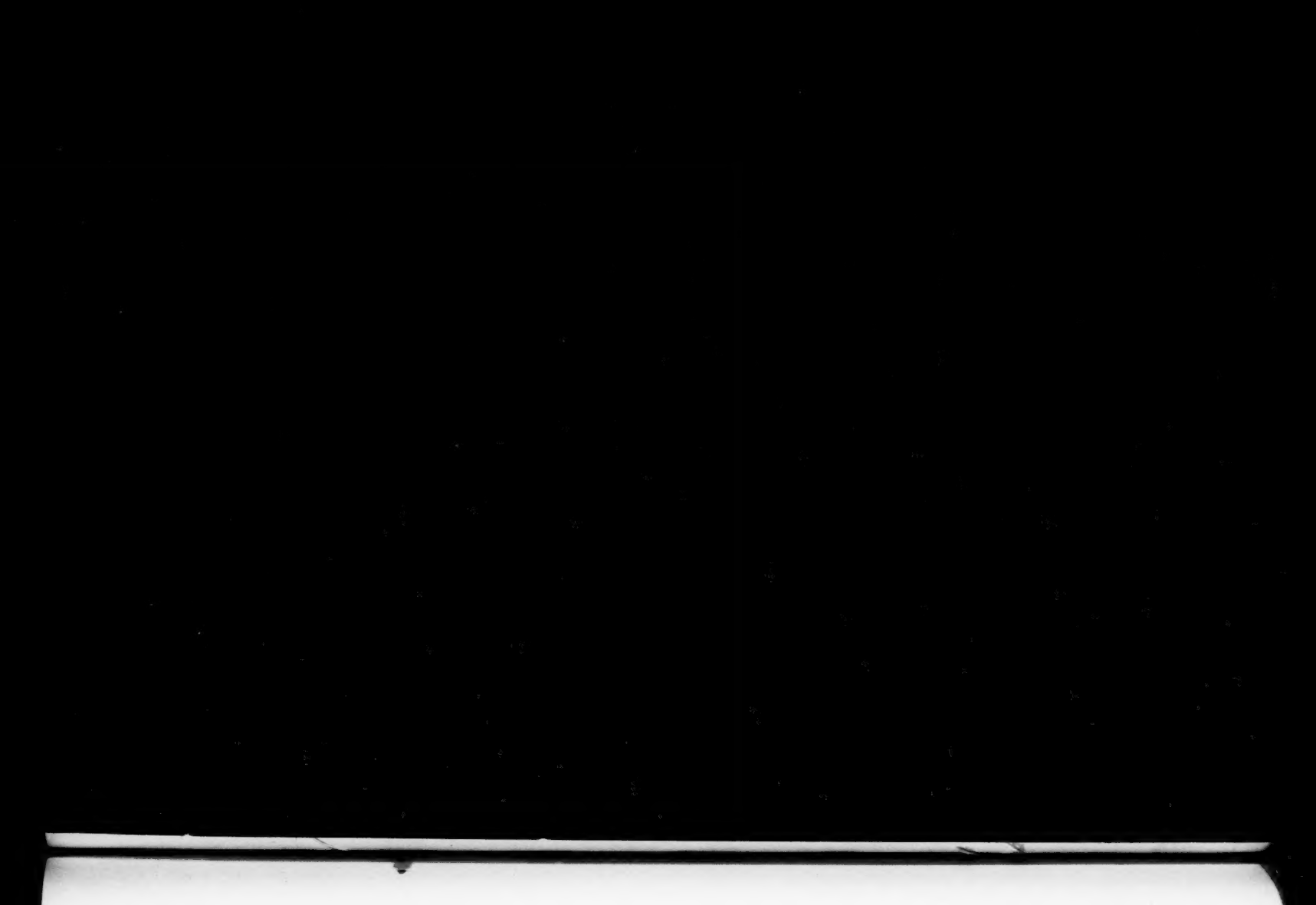
Intelligent selection only accelerates this natural process of progressive variation, for it singles out the individual which is producing gametes of unusual value and permits the union of such high grade gametes only with gametes of their own sort, so that step after step in a particular direction becomes possible, where unguided self-fertilization would give only halting and uncertain progress. Can we doubt that it is progressive varia-

tion guided by rational selection in a particular direction that has made possible the doubling in size that most of our domesticated animals have undergone since they were taken from the wild state? And does any one seriously think that a *single* selection from wild stock has produced for us the enormous horses of Flanders, or the little ponies of the Shetland Isles, the enormous sheep of the Scotch highlands, or the huge rabbits of Europe, each a monstrosity in comparison with its most probable wild ancestors, and yet producing blends in crosses with them? This blending shows that the change has been one of slow accomplishment and not the result of sudden discontinuous change.

When we compare the color varieties of domestic animals with those of their wild ancestors, as I have been able personally to do in the case of cavies, we are struck by the fact that the domestic varieties are relatively clear and distinct in color, either more intense, more dilute, or of purer color than we can obtain from the wild form by simple recombination of genetic factors. For example it is possible by crosses to obtain from wild cavies the retrogressive varieties, black and yellow. But such synthetic blacks lack the full intensity of blackness found in our best strains of black guinea-pigs, and the synthetic yellows are apt to be either pale or muddy in yellowness, lacking the intensity and brilliancy of our best domestic varieties. It is impossible to escape the impression that our improved domestic varieties are not mere factorial recombinations derived from wild species, but that they have been forced up to a higher standard by repeated selection; that the breeder, for example, has first observed variation in intensity of blackness among his blacks (doubtless obtained originally from a retrogressive sport) and that by repeatedly selecting the blackest available individuals he has increased the blackness of the race. Thus it is no accident that the meat and milk and wool producing capacity of our domestic animals far exceeds that of any wild ancestral species. The standard in each case has been raised and it has not been raised by a single lucky accident (the mutation view), but by a series of slow advances each impossible until a previous advance had been made. I am aware indeed that Pearl at one time maintained an opposite view, holding (if I remember correctly) that our best strains of poultry are no better layers than *some* strains of jungle fowl. But I do not believe that this view can be successfully defended. I am certain that such an idea is quite preposterous in

the case of most characters for which our domestic animals are valued and as regards which their *improvement* has been attempted by selection. In such cases there has been a *series* of slight advances, and everything indicates that the *order* of the advances is significant and necessary, that the higher stages can be attained only by passing through the lower ones. If this is so, we need not quibble about "*causation*," but we may assure ourselves that if we wish to attain a distant goal, the first thing to do is to make for intermediate points.

I regard it as a hopeful sign that Pearl can see no reason why genetic changes may not be small in amount in some cases, even though large in others. This I hope is only a first step toward the complete abandonment of that "real, genuine pure-line body of doctrine" which he still holds dear.

W. E. CASTLE

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